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DNA Barcoding and Systematic Review of Minervaryan Frogs (Dicroglossidae: *Minervarya*) of Peninsular India: Resolution of a Taxonomic Conundrum with Description of a New Species

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Abstract The genus *Minervarya* is among the most widely distributed, commonly occurring, and taxonomically confusing groups of dicroglossid frogs in India. Recent studies have provided evidence that this genus contains complexes of morphologically conserved but genetically divergent taxa—some widely distributed across South and Southeast Asia, and many particularly restricted to the Western Ghats region of the Indian Peninsula—posing several challenges in resolving long-standing taxonomic confusions. Here, we present a systematic review of minervaryan species found in Peninsular India, based on extensive DNA barcoding with nearly 400 samples from the entire range of the genus, including 277 new samples and topotypic material for most available names from the study area, combined with detailed morphological studies. As a result, we recognise 18 species in Peninsular India, including a new species described herein as *Minervarya pentali* **sp. nov**. Due to the comprehensive nature of the study, including comparisons with all available types, certain long-standing taxonomic uncertainties on the status of ten previously known taxa are resolved. *Rana* (*Tomopterna*) *parambikulamana* Rao, 1937 (= *Minervarya parambikulamana*), *Rana* (*Hylorana*) *sauriceps* Rao, 1937 (= *Minervarya sauriceps*), and *Fejervarya kudremukhensis* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007" (= *Minervarya kudremukhensis*), are considered as junior subjective synonyms of *Rana (Rana) limnocharis mysorensis* Rao, 1922 (= *Minervarya mysorensis*); *Nyctibatrachus sanctipalustris* var. *modestus* Rao, 1920 (= *Minervarya modesta*) is proposed to be a synonym of *Rana limnocharis syhadrensis* Annandale, 1919 (= *Minervarya syhadrensis*); while *Rana murthii* Pillai, 1979 (= *Minervarya murthii*) and *Fejervarya mudduraja* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007" (= *Minervarya mudduraja*) are considered as junior subjective synonyms of *Rana nilagirica* Jerdon, 1853 (= *Minervarya nilagirica*). At the same time, *Rana brevipalmata* Peters, 1871 (= *Minervarya brevipalmata*), previously known only from its original description and the type specimen, is recognised as a distinct species referable to live populations in the Western Ghats. The study results in taxonomic stability of all the currently recognised members of the genus in Peninsular India. Significant geographical range extensions of species previously known from single localities are also provided based on morphologically and genetically confirmed records. Additionally, we classify all the recognised species into eight species-groups, with the aim of facilitating a better working taxonomy and future systematic studies on minervaryan frogs across their entire known range in Asia.

Keywords amphibia, distribution, *Fejervarya*, integrative taxonomy, *Minervarya pentali* **sp. nov.**, morphology, species groups, Western Ghats Biodiversity Hotspot

1. Introduction

The systematics of the genus *Minervarya* Dubois, Ohler, and Biju, 2001 (sensu lato) has been a subject of considerable discussion in the past few years, primarily owing to the conserved and confusing morphology of its members, as well as the largely unresolved genus-level relationships with the closely related *Fejervarya* Bolkay, 1915 and *Sphaerotheca* Günther, 1859 (e.g., Dinesh *et al.*, 2015; Garg and Biju, 2017; Sanchez *et al.*, 2018). As currently recognised (sensu Sanchez *et al.*, 2018), the genus constitutes a relatively large radiation of small to large-sized species (male SVL 16–50 mm; female SVL 19–65 mm), characterised by the presence of vomerine ridge; presence of

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pineal eye; presence of rictal glands, weakly to well developed (especially in males), and a light greyish-brown glandular stripe extending from the lower half of the tympanum up to the level of the shoulders on either side; presence of fejervaryan lines on either side of the belly; absence of webbing between fingers; presence of webbing between toes, ranging from reduced to extensive but never complete; absence of finger and toe discs; presence of skin folds, either continuous or discontinuous, with glandular warts on the dorsum; and smooth ventral skin (Dubois *et al*., 2001; Garg and Biju, 2017).

The recognised thirty-five species of the genus are predominantly distributed in South Asia (India including the Andaman and Nicobar Archipelago, Sri Lanka, Pakistan, Nepal, Bhutan, and Bangladesh), with only two members found in the Southeast Asian countries of Myanmar and Thailand, and neighbouring regions of southern China (Frost, 2021; Khatiwada *et al*., 2021). Most of these (31 species) are known to occur in India, with the highest diversity (23 species) and endemism (21 species) in the Western Ghats Biodiversity Hotspot, which encompasses the southwest coast of the Indian Peninsula (Dinesh *et al*., 2015; Frost, 2021; Garg and Biju, 2017). However, several species of the region, such as *Minervarya brevipalmata*, *M. modesta*, *M. murthii*, *M. mysorensis*, *M. nilagirica*, *M. parambikulamana*, and *M. sauriceps*, are known only from their original descriptions or type specimens, in the absence of any new collections or reliable reports ever since their descriptions (Garg and Biju, 2017). Although new species of this genus have been described in the recent years, of which 12 species alone are from regions in Peninsular India (e.g., Kuramoto *et al*., 2008 "2007"; Dinesh *et al*., 2015; Garg and Biju, 2017; Raj *et al*., 2018; Phuge *et al*., 2019), attempts to either address or resolve the taxonomic status of the poorly known taxa have been limited. More recently, Garg and Biju (2017) assigned all the Western Ghats species into four morphologically diagnosed species groups. Phuge *et al*. (2020) clarified the taxonomic status of *M. syhadrensis* (Annandale, 1919), also leading to the synonymy of *M. caperata* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008. Khatiwada *et al*. (2021) recently clarified also the taxonomic status and generic placement of *Minervarya* species found in Nepal based new collections along with molecular data, with implications for species found in India. However, the taxonomic status of a large number of named taxa still remains doubtful, thereby deterring proper identification and range delineation of minervaryan frogs, particularly within the Western Ghats. At the same time, integrated morphological and molecular studies based on comprehensive as well as wide taxon sampling for all known species of the genus, such as those undertaken on other groups of frogs in the region (e.g., Biju and Bossuyt, 2009; Biju *et al*., 2011, 2014a, 2014b; Dahanukar *et al*., 2016, 2017; Garg and Biju, 2016; Garg *et al*., 2018, 2019, 2021; Vijayakumar *et al*., 2014), remain unattempted on minervaryan frogs.

We undertook a study on minervaryan frogs, based on sampling of all known species of the genus in Peninsular India over a period of nearly two decades. Here, for the first time, we report specimens for all the recognised species of the region identified based on detailed morphological studies, along with molecular data from 277 newly sampled individuals combined into a DNA barcoding study using mitochondrial 16S rRNA gene sequences. The primary aim of our study was to resolve the taxonomic identities of species, particularly of members known only from their original descriptions and possibly confused with other widespread species. In turn, our wide sampling along with new topotypic material also enabled us to investigate the distribution ranges of species, the presence of potentially undescribed diversity, as well as understand systematic affinities for defining species-groups in this large and taxonomically challenging group of frogs.

2. Materials and Methods

2.1. Field sampling Extensive sampling of *Minervarya* frogs was carried out across Peninsular Indian states, particularly focusing on the Western Ghats region, which is the major centre of diversity and endemism in the genus. Some populations of species that have distributions extending into the Eastern Ghats, and Central and North India were also sampled (Table S1). Since minervaryan frogs occupy a wide range of habitats, our search efforts covered primary and secondary forests, plantations and agricultural fields, as well as other vegetated and wayside open areas close to permanent or temporary water bodies in rural and urban landscapes, right from sea level up to elevations of 2400 m asl. Collections were primarily undertaken at night during the breeding season (June–September) by locating calling males. Individuals were also encountered during opportunistic searches in the night and day time, both within and outside the breeding season. Live specimens were photographed in the wild or in captive conditions, followed by euthanisation in Tricaine methanesulfonate (MS-222) solution. Prior to fixation in 4% formalin, a portion of tissue was extracted either from thigh (adult) or tail muscle (tadpoles), preserved in absolute ethanol, and eventually stored at –20 °C for subsequent molecular studies. The formalin-fixed specimens were later rinsed under running water and transferred to 70% ethanol for preservation. Specimens designated as types in the present study are deposited in the museum of the Bombay Natural History Society (BNHS), Mumbai, India. Referred specimens are available at Systematics Lab, University of Delhi (SDBDU), India. Geographical coordinates and elevation at the sampling localities were recorded on a Garmin 76CSx GPS

using the WGS84 datum system. Maps were prepared using QGIS (http://www.qgis.org).

2.2. Molecular study Genomic DNA was extracted from 277 new samples using Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, CA, USA), following manufacturer's protocol. A fragment of the mitochondrial 16S rRNA gene was PCR-amplified using previously published primer set 16Sar and 16Sbr (Simon *et al*., 1994) and sequenced on both forward and reverse strands with BigDye Terminator v3.1 Cycle Sequencing kit using an ABI 3730 automated DNA sequencer (Applied Biosystems). The raw sequence data was assembled and checked in ChromasPro v1.4 (Technelysium Pty Ltd.), and deposited in the GenBank under accession numbers MZ156076–MZ156352.

In addition to our newly sequenced data, we retrieved 120 homologous sequences for all known *Minervarya* species from the GenBank. *Limnonectes khasianus* was used as an outgroup taxon for the phylogenetic analyses. A dataset of total 398 sequences was assembled in MEGA 7.0 (Kumar *et al*., 2016). Sequences were aligned using the MUSCLE tool (Edgar, 2004) in MEGA 7.0, and the alignment was compared using MAFFT (Madeira *et al*., 2019). The resultant dataset of 544 characters was analysed using the Maximum Likelihood (ML) and Bayesian approaches. The appropriate model of sequence evolution was determined by implementing Akaike Information Criteria in ModelTest 3.4 (Posada and Crandall, 1998). Bayesian analyses were executed in MrBayes (Ronquist and Huelsenbeck, 2003) for five million generations using uniform priors, four Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains, and the best-fit General Time Reversible (GTR) model with a proportion of invariant sites (+I) and gamma-distributed rate variation among sites (+G). Trees were sampled at every 1000th generation and the Bayesian posterior probabilities (BPP) for clades were summarised after discarding the first 25 percent trees as burn-in (Huelsenbeck *et al*., 2001). Clade support was also assessed in the ML framework through 10,000 ultrafast bootstrap replicates (UBS) executed using the GTR+I+G model in IQ-TREE (Minh *et al*., 2013), as implemented on the IQ-TREE webserver (Trifinopoulos *et al*., 2016). Intra- and interspecific uncorrected pairwise genetic distances among species were computed using MEGA 7.0 (Kumar *et al*., 2016).

2.3. Morphological study Morphological comparisons were made with the available type specimens, original descriptions, and new topotypic specimens for all the currently recognised *Minervarya* species known to occur in Peninsular India. The types of following species were examined: *M. agricola* and *M. murthii* (ZSI/SRS—Zoological Survey of India, South Regional Station, Chennai); *M. andamanensis*, *M. modesta*, and *M. syhadrensis* (ZSIC—Zoological Survey of India, Kolkata); *M. brevipalmata* (ZMB—Zoological Museum, Berlin); *M. cepfi*, *M. gomantaki*, *M. kadar*, *M. manoharani*, and *M. neilcoxi* (ZSI/WGRC—Zoological Survey of India, Western Ghats Regional Centre, Kozhikode); *M. goemchi*, *M. kalinga*, *M. krishnan*, and *M. marathi* (ZSI/WRC—Zoological Survey of India, Western Regional Centre, Pune); *M. keralensis* and *M. mysorensis* (NHM—Natural History Museum, London); *M. kudremukhensis* and *M. mudduraja* (BNHS—Bombay Natural History Society, Mumbai); *M. nilagirica*, *M. rufescens*, and *M. sahyadris* (MNHNP—Muséum National d'Histoire Naturelle, Paris). For two species *M. parambikulamana* and *M. sauriceps*, for which type specimens are lost, comparisons were made with the original descriptions and new topotypic specimens. Morphological characters for other congeners with their geographical ranges restricted outside the study region were largely derived from their original descriptions or subsequent literature, available types or other museum specimens, published photographs, or new collections. Shared morphological characters were also identified for grouping of species.

We used only adult (mature) individuals for the morphometric studies. Sex and maturity were determined by the presence of secondary sexual characters (such as nuptial pads and vocal sacs in males) or examination of gonads. Measurements and associated terminologies follow Biju and Bossuyt (2009). The following measurements were taken to the nearest 0.1 mm using digital slide-calipers or a binocular microscope with a micrometer ocular: snout-vent length (SVL), head width (HW, at the angle of the jaws), head length (HL, from rear of mandible to tip of snout), MN (distance from the rear of the mandible to the nostril), MFE (distance from the rear of the mandible to the anterior orbital border), MBE (distance from the rear of the mandible to the posterior orbital border), snout length (SL, from tip of snout to anterior orbital border), eye length (EL, horizontal distance between bony orbital borders), inter upper eyelid width (IUE, the shortest distance between the upper eyelids), maximum upper eyelid width (UEW), internarial distance (IN), internal front of the eyes (IFE, shortest distance between the anterior orbital borders), internal back of the eyes (IBE, shortest distance between the posterior orbital borders), NS (distance from the nostril to the tip of the snout), EN (distance from the front of the eye to the nostril), TYD (greatest tympanum diameter), TYE (distance from the tympanum to the back of the eye), forearm length (FAL, from flexed elbow to base of outer palmar tubercle), hand length (HAL, from base of outer palmar tubercle to tip of third finger), $FL_{I–IV}$ (finger length), thigh length (TL, from vent to knee), shank length (SHL, from knee to heel), foot length (FOL, from base of inner metatarsal tubercle to tip of fourth toe), total foot length (TFOL, from heel to tip of fourth toe), FD (maximum disc width of finger), width of finger (FW, measured at the base of the disc), TD (maximum disc width of toe), width

of toe (TW, measured at the base of the disc). Digit number is represented by roman numerals I–V in subscript. Measurements and photographs were largely taken of the right side of the specimen, and sometimes on the left side when a character was damaged. All measurements provided in the taxonomy section are in millimetres. For the convenience of discussion, species of the genus *Minervarya* are categorised based on their body size, as modified from Garg and Biju (2017): small (male SVL 16.0–25.0 mm), medium (male SVL 25.1–45.0 mm) and large (male SVL 45.1–65.0 mm).

2.4. ZooBank registration This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank LSID (Life Science Identifier) for this publication is urn:lsid:zoobank.org:pub:3D20A723-AA21-456E-9C95-F3DF0F56A2FC and for the new species described herein LSID is urn:lsid:zoobank.org:act:1CBAF3D4-17A1-4A1F-B1A1-8E58A17C8FF9. The LSIDs and associated information can be resolved through any standard web browser by appending the LSID to the prefix http://zoobank.org.

3. Results

3.1. DNA barcoding and phylogenetic relationships The results of our BI and ML phylogenetic analyses were highly congruent with respect to the monophyly of the major well-supported clades. We recovered 26 species-level lineages (representing recognised or potential species) within the genus *Minervarya* (Figure 1). Our 277 new samples nested with 12 previously known species identified from topotypic material. Of the total 24 previously recognised species in the genus represented on the tree, 16 were found in the Western Ghats or the Indian Peninsula. Of these, 13 species were restricted to the region, while three species had their distributions extending towards central, eastern, and northern Indian regions (Table S1). In addition, our analyses recovered two hitherto unrecognised lineages—one identified as belonging to *Minervarya brevipalmata* (see section '3.2 Taxonomic status of some nominal taxa'), and the other representing a new species (formally described as *Minervarya pentali* **sp. nov.** under the section '3.3 Description of a new species'). The species-level relationships were largely in agreement with previous studies (Dinesh *et al.*, 2015; Garg and Biju, 2017; Köhler *et al.*, 2019; Phuge *et al.*, 2019; Raj *et al.*, 2018; Sanchez *et al.*, 2018), and differed primarily with respect to either the level of support received for various clades or their taxonomic identities (as clarified in the subsequent section '3.2 Taxonomic status of some nominal taxa'). Twenty species recovered as highly supported (BPP ≥ 95, UBS ≥ 90) monophyletic clusters both in the BI and ML analyses (IQ-TREE) included *M. sahyadris*, *M. krishnan*, *M. agricola*, *M. asmati*, *M. teraiensis* (based on conspecific sequence identity with the typical sequences of *M. dhaka*, as per sequences available from Howlader *et al.*, 2016; Khatiwada *et al.*, 2021), *M. chiangmaiensis*, *M. syhadrensis*, *M. pentali* **sp. nov.**, *M. brevipalmata*, *M. goemchi*, *M. mysorensis*, *M. kirtisinghei*, *M. manoharani*, *M. cepfi*, *M. neilcoxi*, *M. marathi*, *M. muangkanensis*, *M. keralensis*, *M. kalinga*, and *M. nilagirica*. The only exceptions were: (1) *M. gomantaki*, for which the typical populations from Goa were recovered as a well-supported cluster (BPP 100, UBS 99), however, the relationship of other genetically and geographically close populations from Maharashtra, which were also morphologically referable to this species, remained unresolved in both the analyses; and (2) *M. rufescens*, for which the monophyly of all the assigned populations was highly supported in our BI (BPP 100) but moderately supported in the ML analysis (UBS 80). Furthermore, the clade support could not be assessed for four species currently represented by a single GenBank sequence each (*M. nepalensis*, *M. greenii*, *M. kadar*, and *M. andamanensis*).

All the *Minervarya* species included in our phylogenetic analyses were recovered in eight distinct, largely well supported, and some moderately supported (BPP ≥ 90, UBS ≥ 70) clades representing species-groups—(1) *Minervarya sahyadris* group: *M. gomantaki*, *M. krishnan*, and *M. sahyadris*; (2) *Minervarya syhadrensis* group: *M. syhadrensis*, *M. nepalensis* (sensu Khatiwada *et al.*, 2021), and *M. pentali* **sp. nov.**; (3) *Minervarya agricola* group: *M. agricola*, *M. asmati*, *M. chiangmaiensis*, and *M. teraiensis*; (4) *Minervarya mysorensis* group: *M. brevipalmata*, *M. goemchi*, and *M. mysorensis*; (5) *Minervarya rufescens* group: *M. cepfi*, *M. kadar*, *M. manoharani*, *M. neilcoxi*, and *M. rufescens*; (6) *Minervarya andamanensis* group: *M. andamanensis* and *M. muangkanensis*; (7) *Minervarya greenii* group: *M. greenii* and *M. kirtisinghei*; (8) *Minervarya nilagirica* group: *M. kalinga*, *M. keralensis*, and *M. nilagirica*. Based on further morphological studies, these clades are herein defined as species-groups, primarily adapted and expanded from our previous work (Garg and Biju, 2017). A single species, *M. marathi* was provisionally assigned to the *Minervarya andamanensis* group based on morphology, although it showed a deeply divergent yet highly to moderately supported sister-group relationship with members of the morphologically disparate *Minervarya rufescens* group.

Among the recognised species-groups, several notable intra- and inter-group relationships were observed. Within the *Minervarya sahyadris* group, *M. sahyadris* comprised of two well-supported divergent sub-lineages (uncorrected *p*-distances ranging between 1.3%–1.8%) from localities in Karnataka and Kerala, respectively (Figures 1 and 2). This species showed a well-supported sister-group relationship with the clade containing two weakly resolved but divergent sub-populations of *M. gomantaki* from Goa and Maharashtra (uncorrected

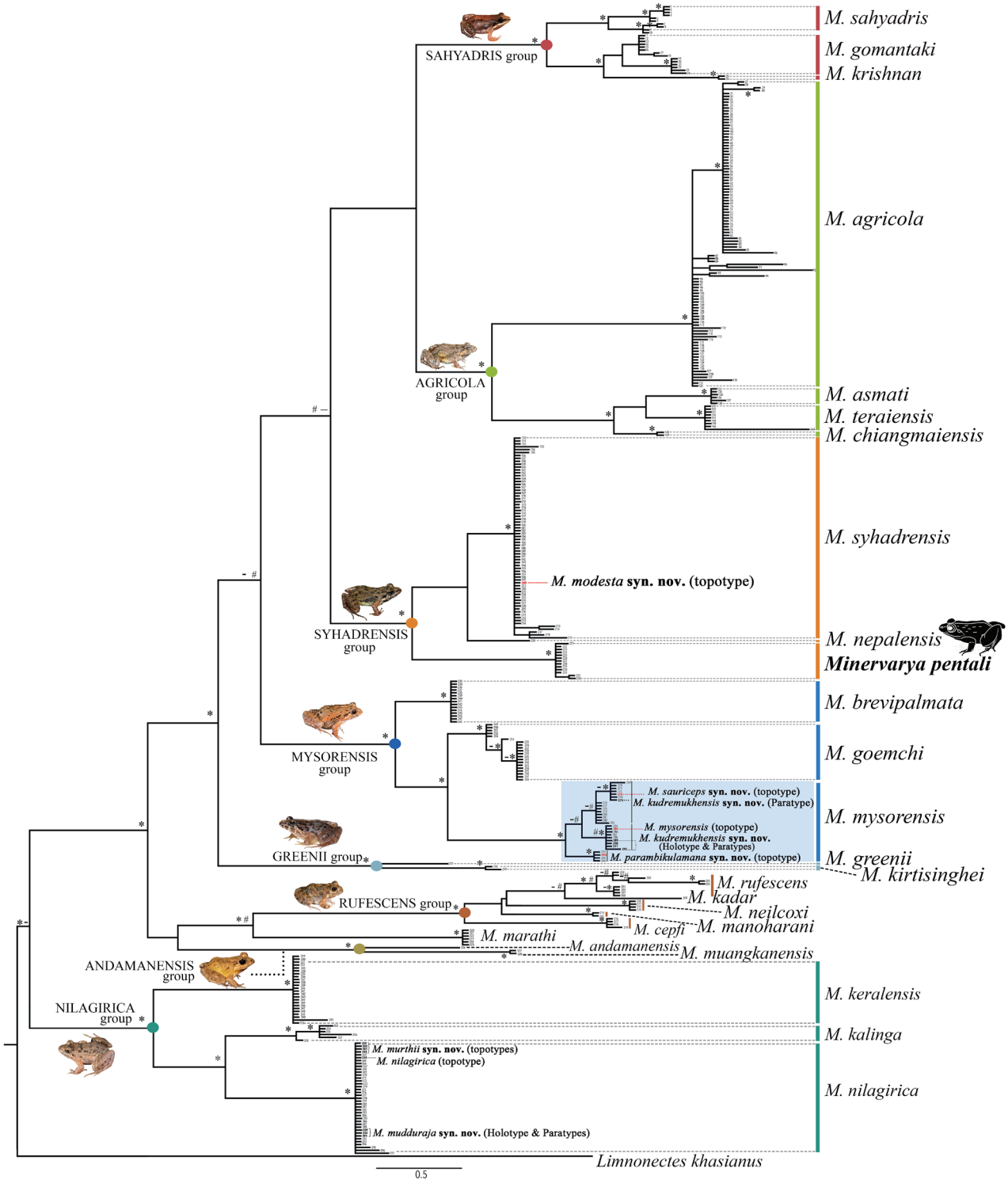

Figure 1 Bayesian consensus phylogram depicting phylogenetic relationships among 397 *Minervarya* samples from regions across the known range of the genus in Asia based on mitochondrial 16S rRNA sequences. The focal genus *Minervarya* is represented by 25 previously known and one new species, comprising eight species-groups discussed in the study. Coloured vertical bars alongside the terminal nodes indicate species; bold letters indicate the new species; and coloured circles at the internal nodes indicate species-groups. Asterisk symbol (*) above the branch indicates Bayesian Posterior Probabilities (BPP) ≥ 95% and Ultrafast Bootstrap Support (UBS) values ≥ 90%; hash symbol (#) indicates BPP ≥ 90% and UBS values ≥ 70%; dash (-) indicates branches with BPP < 90% or UBS < 70% in cases where BPP ≥ 90% or UBS ≥ 70% in one of the analyses. The tree is rooted with *Limnonectes khasianus* as the outgroup taxon.

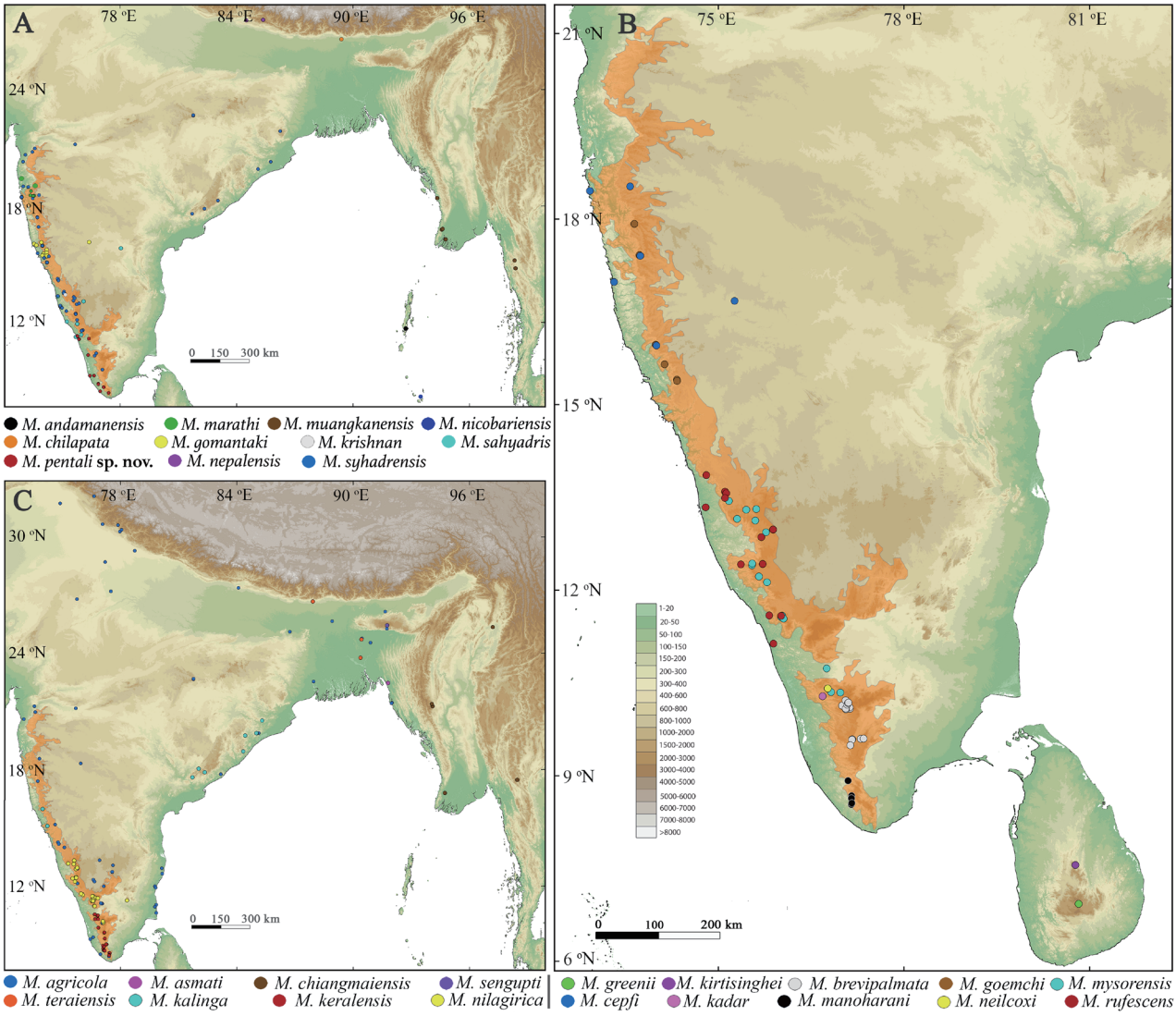

Figure 2 Geographical distribution of twenty-nine species in the genus *Minervarya* based on genetic samples used in the study and the known type localities. (A) Eleven species of the *Minervarya andamanensis* group (*M. andamanensis*, *M. marathi*, *M. muangkanensis*, and *M. nicobariensis*), *Minervarya sahyadris* group (*M. chilapata*, *M. gomantaki*, *M. krishnan*, and *M. sahyadris*), and *Minervarya syhadrensis* groups (*M. pentali* **sp. nov.**, *M. nepalensis*, and *M. syhadrensis*); (B) Eight species of the *Minervarya agricola* group (*M. agricola*, *M. asmati*, *M. chiangmaiensis*, *M. sengupti*, and *M. teraiensis*) and *Minervarya nilagirica* group (*M. kalinga*, *M. keralensis*, and *M. nilagirica*); (C) Ten species of the *Minervarya greenii* group (*M. greenii* and *M. kirtisinghei*), *Minervarya mysorensis* group (*M. brevipalmata*, *M. goemchi*, and *M. mysorensis*), and *Minervarya rufescens* group (*M. cepfi*, *M. kadar*, *M. manoharani*, *M. neilcoxi*, and *M. rufescens*).

p-distance ranging between 1.1%–1.7%) and *M. krishnan*. A sister-group relationship between *Minervarya sahyadris* group and the *Minervarya agricola* group was recovered in the BI analysis with low support (BPP 82), whereas the ML analysis suggested a possible sister relationship between the *Minervarya sahyadris* group and *Minervarya syhadrensis* group, albeit with much lower confidence (UBS 54, not shown). However, the close relationship of these three groups received moderate to weak support in our analyses (BPP 93, UBS 56). Within the *Minervarya agricola* group, a sister-group relationship between *M. asmati* and *M. teraiensis* was recovered in BI with low support (BPP 61), but together the two species showed a well-supported sister-group relationship with *M. chiangmaiensis*. These three species were more distantly related to *M. agricola*, which also showed high levels of genetic differentiation (uncorrected *p*-distances ranging between 0.6%–4.0%) among various poorly resolved population sub-clusters, largely with either south-ranging (Tamil Nadu, Kerala, and Karnataka) or north-ranging (Maharashtra, Andhra Pradesh, Gujarat, Rajasthan, Punjab, Himachal Pradesh, Haryana, Delhi, Uttar

Pradesh, Uttarakhand, Madhya Pradesh, Chhattisgarh, Odisha, Bihar, up to West Bengal) distribution pattern. The findings suggest that *M. agricola* could possibly also represent a complex of multiple species requiring further detailed population studies. Within the *Minervarya syhadrensis* group, the relationships between three recognised species received low support, but were suggestive of a sister relationship between *M. syhadrensis* and *M. nepalensis* (BPP 74, UBS <50), which were together likely to form the sister-group to the new species *M. pentali* **sp. nov.** At the same time, intraspecific divergence among the various widely distributed *M. syhadrensis* populations (from Kerala, Karnataka, Goa, Maharashtra, Gujarat, Andhra Pradesh, Madhya Pradesh, up to Odisha) reached up to 1.2%. The otherwise well-supported and distinct *Minervarya brevipalmata* group was recovered as having a weakly supported and unresolved relationship with three groups (*Minervarya sahyadris* group, *Minervarya syhadrensis* group, and *Minervarya agricola* group). Within the *Minervarya brevipalmata* group, *M. mysorensis* and *M. goemchi* showed a well-supported sister relationship, and together the two species formed a sister-group relationship with *M. brevipalmata* with high support (the taxonomic identities of these taxa are discussed in the section '3.2 Taxonomic status of some nominal taxa'). The intraspecific divergence among the various populations of *M. mysorensis* ranged up to 1.1% between three major population sub-clusters: (1) Anaimalais up to Nelliyampathy hills encompassing regions south of Palghat gap in Kerala and Tamil Nadu; (2) Wayanad plateau in northern Kerala up to Coorg plateau in southern Karnataka; and (3) Chikamagalur hills up to Sharavathi basin. For *M. goemchi*, the observed intraspecific divergences were up to 0.4% among populations distributed from northern Karnataka up to Maharashtra. On the other hand, the distribution of *M. brevipalmata* was restricted to regions south of the Palghat gap, from Anamalai and Cardamom hills down to Meghamalais. The *Minervarya greenii* group, comprising two species endemic to Sri Lanka, was recovered as having a sister relationship with the clade containing four groups (*Minervarya sahyadris* group, *Minervarya syhadrensis* group, *Minervarya agricola* group, and *Minervarya brevipalmata* group). The *Minervarya rufescens* group showed a well-supported sister-group relationship with *M. marathi*. Together, these members were recovered as having a close relationship with the *Minervarya andamanensis* group, albeit with weak support. The *Minervarya nilagirica* group formed the most distinct clade in the genus with a basal relationship to all the remaining known *Minervarya* species and species groups. Within the *Minervarya nilagirica* group, the sister relationship between *M. nilagirica* (predominantly restricted to the Western Ghats regions of Tamil Nadu, Kerala, and Karnataka) and *M. kalinga* (currently known from the northern Western Ghats states of Goa and Maharashtra, and also from the Eastern Ghats regions in Andhra Pradesh and Odisha, with intraspecific divergences of up to 1.1%) was well supported. The third member of the group, *M. keralensis* (restricted to south of the Palghat gap in Kerala and Tamil Nadu), formed a sister-group to *M. nilagirica* and *M. kalinga* with high support (Figures 1 and 2). Although no other previous comparable study on minervaryan frogs of Peninsular India is available in terms of taxon sampling, the relationships recovered in our phylogenetic analyses among the major clades were largely congruent with the recent multi-gene and mitochondrial 16S rRNA phylogenies (e.g., Dinesh *et al.*, 2015; Garg and Biju, 2017; Köhler *et al.*, 2019; Phuge *et al.*, 2019; Raj *et al.*, 2018; Sanchez *et al.*, 2018).

3.2. Taxonomic status of ten nominal taxa

***Minervarya brevipalmata* (Peters, 1871): taxonomic identity and nomenclatural stability.** While describing this species as *Rana brevipalmata*, Peters (1871) provided a detailed description of the holotype (Figure 3), which he stated to have been purchased from Pegü (Burma, Myanmar). Boulenger (1905 "1904") doubted the type locality of this taxon, apparently due to the availability of several comparable specimens "from the Nilgherry and Travancore hills" in southern India, which he identified as belonging to *Rana brevipalmata* Peters, 1871. Subsequently, this taxon was subjected to frequent taxonomic changes. Boulenger (1890) synonymised it under *Rana limnocharis* Gravenhorst, 1829 and referred to it as "var. *brevipalmata*" based on examination of some specimens from "Pegu and S. India". Subsequent authors (e.g., Annandale, 1917; Boulenger, 1920; Roux, 1928; Bourret, 1942; Gorham, 1974; Daniel, 1975) followed this by treating it either as a subspecies or a junior subjective synonym of *Rana limnocharis*. Pillai (1980) specifically addressed the taxonomic status of this taxon. Based on multiple new collections from Kerala and Tamil Nadu, he discussed morphological characters as well as behavioural patterns distinguishing *Rana brevipalmata* as a distinct species from *Rana limnocharis nilagirica*, with which he stated it to have been previously confused (Boulenger, 1920). However, Dubois (1984) considered *Rana brevipalmata* to be a junior subjective synonym of *Rana nilagirica* Jerdon, 1853, but subsequently treated it as *incertae sedis* in the genus *Fejervarya* (Dubois, 1987 "1986"). Dubois and Ohler (2000) later concluded that this name does not refer to any biological species of frog. Yet, *Rana brevipalmata* Peters, 1871 continued to be treated as a valid species, in various genera such as *Limnonectes* (Dubois, 1987; Dutta and Singh, 1996), *Fejervarya* (Iskandar, 1998; Fei *et al.*, 2002; Dinesh *et al.*, 2015), *Zakerana* (Howlader, 2011), and the most recent transfer to *Minervarya* based on the separation of this predominantly South Asian genus from the largely Southeast Asian *Fejervarya* (Sanchez *et al.*, 2018). Most available literature includes this species in the list of Western Ghats frogs, where it is also believed to be restricted (e.g., Daniels, 2005; Dinesh *et al.*, 2009; Dutta, 1997; Frost, 2021). However, none of

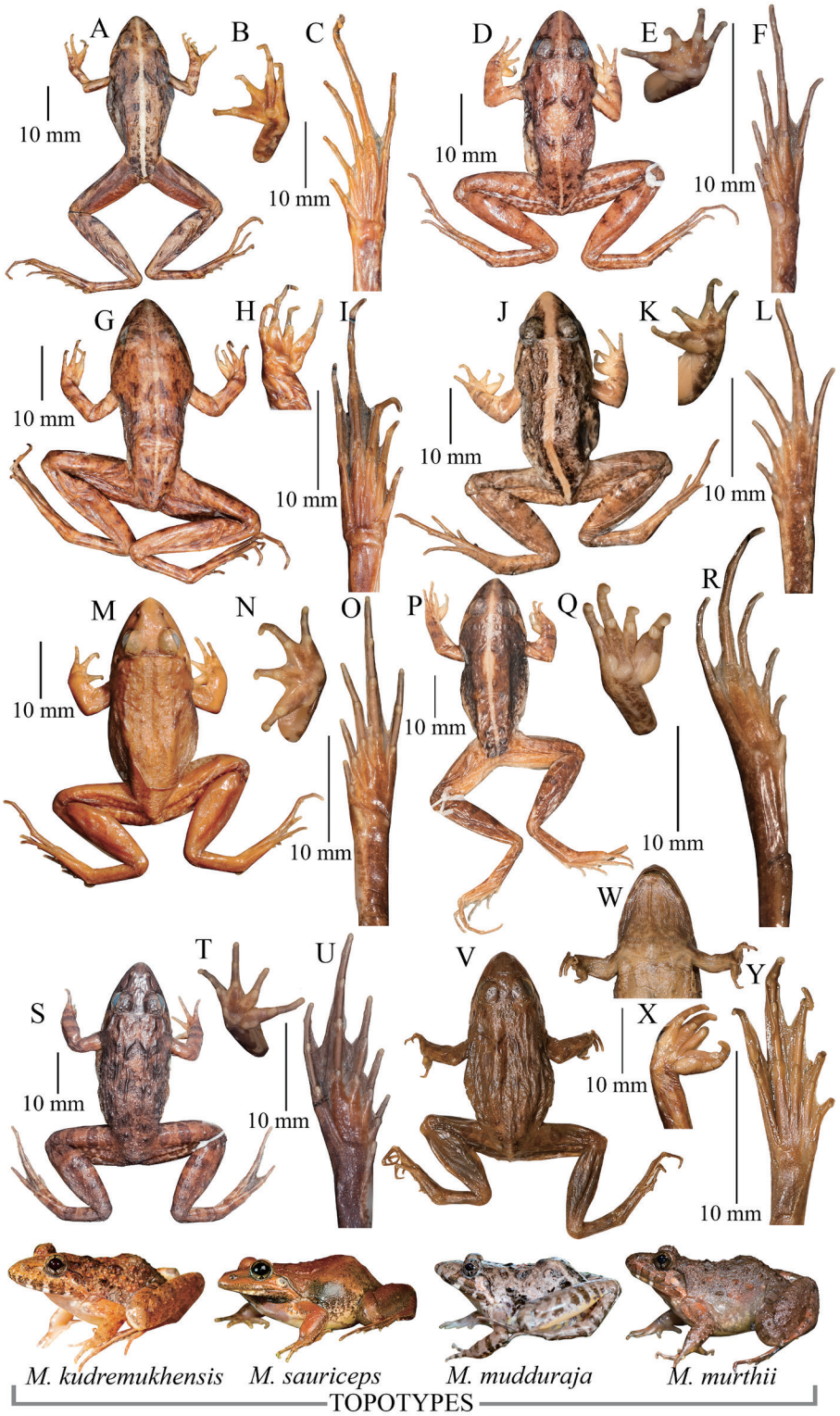

Figure 3 Type specimens of eight *Minervarya* taxa described from Peninsular India showing (left to right) dorsal view, ventral view of hand, and ventral view of foot. (A–C) holotype (ZMB 6130) of *Rana brevipalmata*; (D–F) holotype (BNHS 4653) of *Fejervarya kudremukhensis*; (G–I) holotype (BMNH 1947.2.1.80) of *Rana (Rana) limnocharis mysorensis*; (J–L) neotype (BNHS 6113) of *Rana (Tomopterna) parambikulamana*; (M–O) neotype (BNHS 6114) of *Rana (Hylorana) sauriceps*; (P–R) neotype (MNHNP 1984.2340) of *Rana nilagirica*; (S–U) holotype (BNHS 4645) of *Fejervarya mudduraja*; (V–Y) holotype (ZSI-SRS VA/773) of *Rana murthii*, (W) ventral view of throat and chest showing the absence of "pearl-like papillae". Bottom row: Topotypes of four synonymised nomen in life.

the recent studies have revisited the identity of this taxon and provided new collections or insights on its taxonomic status. Also surprisingly, even though the type of *Rana brevipalmata* was originally stated to have originated from Myanmar, it appears to have been included in the region's amphibian inventories only rarely (Frost, 2021), including its absence from a recent comprehensive study on *Fejervarya* and *Minervarya* frogs of that country (Köhler *et al.*, 2019).

We studied the type specimen of *Rana brevipalmata* Peters, 1871 (ZMB 6130, an adult male) in order to compare it with various populations of minervaryan frogs from the Western Ghats. While describing this taxon, Peters (1871) provided a brief comparison with "*Rana limnocharis* Boie (*Rana gracilis* Wiegm.)" and "the South African *Rana grayi* and *Rana fasciata*", primarily distinguishing it based on very elongated limbs and reduced webbing between toes from the former, and well developed vomerine teeth from the latter species. Altogether, Peters (1871) described a number of morphological characters for *Rana brevipalmata* including head dimensions, position of nostril, tympanum diameter, presence of vomerine teeth, tongue shape, long limbs, relative length of fingers, extent of webbing on foot, skin texture (including dorsal skin with some short longitudinal folds and small rounded tubercles), body colouration and markings (including a bright mid dorsal line), and some body measurements, which were largely found to be matching with the available type. Boulenger (1890) discussed two characters distinguishing var. *brevipalmata* from *Rana limnocharis*: tibio-tarsal articulation "reaching considerably beyond the end of the snout" and foot measuring "two thirds the distance between the end of the snout and the vent." Boulenger (1920) also stated the first finger to be longer than the second in *Rana brevipalmata*. Later, Pillai (1980) studied populations from "Muthanga", and "Chedleth" of Wayanad, Kerala state and "Anamalai" and "Valparai" of Anaimalai Hills, Tamil Nadu state, and provided further comparison between *Rana brevipalmata* from *Rana limnocharis* mainly stating differences in reduced foot webbing, absence of dermal fringe along toe V, tympanum less than half the diameter of the eye, and the tympanum-eye distance equal to the tympanum diameter. We found most of the characters discussed by Boulenger (1890, 1920) and Pillai (1980), as well as several characters discussed in the original description provided by Peters (1871), to be comparable with our multiple new collections from Idukki district of Peninsular India (Table S1), which were also recovered as a distinct and previously unnamed clade within the genus *Minervarya* (Figure 1). Particularly notable among these are characters such as dorsal skin with relatively long longitudinal folds and small rounded tubercles, long hind limbs, reduced webbing between toes, and well developed inner metatarsal tubercle. Hence, building on the judgements made by previous researchers and the additional evidence gathered in the present study, we provisionally consider this taxon to have originated from the Western Ghats and identify live populations referable to this species (Table S1), thereby clarifying its taxonomic status.

***Minervarya mysorensis* (Rao, 1922): rediscovery and revalidation.** This taxon was originally described as a variety *Rana (Rana) limnocharis mysorensis* Rao, 1922 based on two specimens, of which one was mentioned as "Type" "presented to British Museum". The specimen available at NHM (BMNH 1947.2.1.80, an adult male, from Jog, Shimoga, Karnataka) was considered as the holotype (Dutta, 1997). Dutta and Singh (1996) also provided details of the holotype and considered this taxon as a distinct species. However, the species has not been recorded since its original description, other than being included in regional checklists, and is known only from its type locality. We examined the available type specimen at NHM (Figure 3) and along with the characters stated in its original description, compared it with our new collections from the region; particularly a topotypic specimen rediscovered from the originally stated locality. We found our new collection from "Jog" (SDBDU 2001.1332) to be comparable both with the type and the description (Rao, 1922) in numerous respects (measurements for topotype stated in parentheses), such as "From tip of snout to vent" "36.5" mm (SVL 38.2 mm), "snout pointed" (subelliptical to pointed in dorsal and ventral view), "snout longer than the diameter of the eye" (SL 6.2 mm, EL 4.0 mm), "nostril nearer the tip of the snout" (NS 2.5 mm, EN 3.1 mm), "internasal width equals the interorbital space" which is much less than the upper eyelid" (IN 2.7 mm, IUE 2.5 mm), "Tympanum distinct, ½ to ⅜ the diameter of the eye" (TYD 2.0 mm, EL 4.0 mm), "Fingers blunt", "first longer than the second" (FL_I 4.9 mm, FL_{II} 3.5 mm), "Toes slightly swollen at the tips, less than half-webbed" (webbing formula: I2–2II2$^-$–3III2½–3½IV3½–2$^+$V). We also report molecular data for the topotypic and 22 additional populations from regions in the Western Ghats. The integrated molecular and morphological evidence from our study results in the following major findings: (1) rediscovery of *Rana (Rana) limnocharis mysorensis* Rao, 1922 with clarity on the recognition of this taxon as *Minervarya mysorensis* (Rao, 1922); (2) significant range extension of the species based on morphologically and genetically identified records from several localities in Karnataka, Kerala, and Tamil Nadu (Table S1; Figure 2); and (3) clarity on the identity and taxonomic status of three other nominal taxa from the Western Ghats—*Rana (Tomopterna) parambikulamana* Rao, 1937 (= *Minervarya parambikulamana*), *Rana (Hylorana) sauriceps* Rao, 1937 (=*Minervarya sauriceps*), and *Fejervarya kudremukhensis* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007" (=*Minervarya kudremukhensis*)—all of which are revealed to be junior subjective synonyms of *Minervarya mysorensis* (Rao,

1922), with formal actions of synonymy undertaken below in the subsequent sections.

***Minervarya parambikulamana* (Rao, 1937): rediscovery, neotypification, and synonymy.** This taxon was originally described as *Rana (Tomopterna) parambikulamana* Rao, 1937 based on a single specimen from "Parambikulam forests", with an accompanying illustration. This type specimen is considered lost (Dubois, 1984) owing to which the species is currently known only from its original description. The generic placement of this species has been confusing due to its vague description with assignment to the subgenus *Tomopterna* (Rao, 1937), where it continued to be placed by several subsequent authors (e.g., Dutta, 1997; Chanda, 2002; Matsui *et al*., 2008). It was also proposed as *incertae sedis* within *Fejervarya* (Dubois, 1987 "1986") or stated to be "invalid" (Purkayastha and Matsui, 2012), both without discussion. These confusions probably stemmed from Rao's observations (1937): "I have compared this specimen with *R. rufescens, R. breviceps* and *R. dobsoni*, from which it differs almost in every character, and generally resembles *R. tigrina* in external form, though differing in details both from this species and *R. limnocharis* (Forma typica) through which this new species is derivable." Nonetheless, even though the species appears to have been confused with members belonging to five different genera, its assignment to *Minervarya*, as presently understood, can be considered more conclusive based on characters such as head longer than broad, snout pointed, projecting beyond the lower jaw; distinct tympanum; fourth toe considerably longer than the thigh or tibia; and presence of inverted "U" or "V" shaped skin fold, all of which are clearly comparable with the illustration of the type provided by Rao (1937). Within the genus *Minervarya*, this taxon cannot be a member of *Minervarya rufescens* group due to its large snout-vent size, presence of "light vertebral band", "Hind limb long, the tibio-tarsal articulation reaching far beyond the tip of the snout", "inner metatarsal tubercle large smaller than the first toe", head "distinctly longer than broad", and "snout longer than eye". Instead, the species can be assigned to the *Minervarya mysorensis* group (see group definition in the section '3.4 Grouping of species in the genus *Minervarya*') due to its adult size "39.00" mm, "head longer than broad", "Hind limb long, the tibio-tarsal articulation reaching far beyond the tip of the snout", "fourth toe considerably longer than the thigh or tibia", toes "¼ webbed", "inner metatarsal tubercle large", and dorsum with "a light vertebral band" and "cutaneous folds edged black".

Furthermore, our field studies at Parambikulam have resulted in the collection of a species of the genus *Minervarya* that is comparable to many of the characters mentioned and illustrated in the original description of *M. parambikulamana* (Rao, 1937). We provide a description of this new specimen and further find it necessary to designate the same as a neotype of *Rana* (*Tomopterna*) *parambikulamana* Rao, 1937 in accordance with Article 75 of the ICZN (International Commission on Zoological Nomenclature 1999, hereafter, The Code), owing to the following reasons: (1) The unavailability of its name bearing type (Dubois, 1984; Biju, 2001; present study). (2) In the absence of a type, direct evidence on the holotype of *Rana* (*Tomopterna*) *parambikulamana* currently exists only from the original description and accompanying figure (Rao, 1937). However, the description by Rao (1937) is imprecise and not particularly informative, except for a handful of characters such as presence of inverted "U" or "V" shaped skin fold on the dorsum and "inner metatarsal tubercle large smaller than the first toe". These characters also largely overlap with other recognised and morphologically cryptic congeners, especially *M. brevipalmata* (Peters, 1871), *M. mysorensis* (Rao, 1920), *M. sauriceps* (Rao, 1937), and *M. kudremukhensis* (Kuramoto *et al*., 2008 "2007"), some of which in addition have overlapping or close distribution ranges. (3) Further, while describing this species Rao (1937) stated its overall resemblance with two taxa that are now known to be morphologically unrelated, *Rana tigrina* (= *Hoplobatrachus tigerinus*) and *R. limnocharis* (= *Fejervarya limnocharis*). This adds to the confusion in diagnosing *Rana* (*Tomopterna*) *parambikulamana* solely based on its original description. (4) Moreover, the identity and the specific taxonomic status of *Rana* (*Tomopterna*) *parambikulamana* itself have been previously doubted, with authors proposing it to be either *incertae sedis* (Dubois, 1987 "1986") or invalid (Purkayastha and Matsui, 2012) probably due to the difficulty in assigning it to any known living population since its single original record. Hence, based on new evidence gathered in the present study, designation of a neotype is considered essential for defining this taxon objectively, in order to identify it properly from other close congeners, as well as to stabilise the taxonomic status of the nomen. We hereby designate BNHS 6113 from the original type locality "Parambikulam" as the neotype of *Rana (Tomopterna) parambikulamana* Rao, 1937 (= *Minervarya parambikulamama*). The neotype description provided below is largely consistent with what is known of the former name-bearing type.

Description of neotype of *Rana* (*Tomopterna*) *parambikulamana* Rao, 1937. By present designation, Neotype: BNHS 6113 (Figure 3), from Parambikulam, Kerala state, India, collected by S. D. Biju and Sonali Garg on 8 July 2015. A medium-sized adult male (SVL 38.1); head longer (HL 14.6) than wide (HW 12.3); snout sub-elliptical in dorsal and ventral view, obtuse in lateral view, its length (SL 6.5) longer than horizontal diameter of eye (EL 4.7); loreal region obtuse and concave with indistinct canthus rostralis; interorbital space narrower (IUE 2.5) than upper eyelid width (UEW 3.2) and the internarial distance (IN 3.6); tympanum vertically oval, its horizontal diameter (TYD 2.1) slightly more than two-

fifth (44.7%) of the eye diameter (EL 4.7); forearm (FAL 6.1) shorter than hand length (HAL 8.8); outer, inner, and middle metacarpal tubercles present on hand, well developed; thigh (TL 19.6) shorter than shank (SHL 21.7) and foot (FOL 24.1); foot webbing small: I1–2II2^{-}–3III2½–3½IV3½–2^{+}V; inner metatarsal tubercle prominent (IMT 2.2), oval, raised; outer metatarsal tubercle small, rounded. Dorsal skin shagreened to sparsely granular with short longitudinal skin folds; an inverted "V"-shaped ridge on anterior half of the dorsum, at the level of forearms; flanks shagreened to sparsely granular; fore- and hind limbs shagreened or sparsely granular. Ventral surfaces of throat and chest smooth to shagreened; posterior part of belly and thighs granular, and posterior surface of thighs coarsely granular. *Colour in preservation*. Dorsal colouration light greyish-brown; presence of a thick buff-coloured mid-dorsal line extending from the tip of snout to the vent; margins of the dorsal skin folds blackish-brown; upper and lower jaw with faint vertical bands; upper half of tympanum and inner margins of supratympanic fold light brown; flank with faint greyish-brown spots; fore-and hind limbs (including fingers and toes) with dark brownish-black cross bands; dorsal surfaces of posterior half of thigh light brown with buff-coloured reticulations. Ventral surface greyish-white with a yellow tinge.

Synonymisation of *Rana (Tomopterna) parambikulamana* Rao, 1937. Due to the comprehensive nature of our study, we also compared our new collections of *Rana (Tomopterna) parambikulamana* Rao, 1937 (= *Minervarya parambikulamama*) with all other known *Minervarya* species sampled from regions across Peninsular India. Based on a detailed morphological comparison of the original description and new topotypic material, including the designated neotype, we find this taxon to be extremely similar to *M. mysorensis* Rao, 1922 with overlapping morphological traits, which do not support the two taxa to be reliably distinguished from each other. These include characters such as the adult size, snout sub-elliptical to pointed in dorsal and ventral view; short discontinued dorsal skin folds without a constant pattern; presence of an inverted "V"-shaped skin fold at the centre of the dorsum; foot including toes relatively long; and reduced webbing between toes. The skin texture disparity between Rao's description of *M. parambikulamana* and *M. mysorensis* is probably a misinterpretation due to the dehydrated condition of the described specimen, as evident from the illustration (Rao, 1937, Figure 1). In addition, we also sequenced molecular data from the neotype specimen of *M. parambikulamana* and included it in our phylogenetic analyses to further clarify the genealogical affinities of this taxon. Our results find *M. parambikulamana* to be nested together with various populations of *M. mysorensis*, including *M. kudremukhensis* and *M. sauriceps* (both subsequently synonymised with *M. mysorensis*), with shallow genetic distances of 0.8%–1.1%, which not only fall within the range of intraspecific distances observed for the various *Minervarya* species in our study (Table 1), but also do not correspond to any reliable morphological characters for interspecific comparison and may therefore be considered as intraspecific variations. Hence, in accordance with the Article 23 (Principle of Priority) of The Code we consider *Rana (Tomopterna) parambikulamana* Rao, 1937 (= *Minervarya parambikulamana*) as a junior subjective synonym of *Rana (Rana) limnocharis mysorensis* Rao, 1922 (= *Minervarya mysorensis*).

***Minervarya sauriceps* (Rao, 1937): rediscovery, neotypification, and synonymy.** This taxon was originally described as *Rana (Hylorana) sauriceps* Rao, 1937 based on "A number of specimens of all ages" from "Wattekole, Coorg, S. India". However, the original description included measurements only for a single specimen with SVL measuring "30.00 mm", along with illustrations (Rao, 1937). Ever since, there have been no new reports or collections of this species, either from the type locality or other regions. Further, the original name-bearing type is considered lost (Dubois, 1984), hence this nominal taxon was known only from its original description. Our surveys within the region of the type locality "Wattakole" (= Watekolli) resulted in collection of a 'chocolate red' coloured specimen belonging to a species of the genus *Minervarya* (Figure 3) that is found to be comparable with the original description and accompanying illustrations of *Rana (Hylorana) sauriceps* Rao, 1937 with respect to several characters such as "hind limbs rather long, slender, tibio-tarsal articulation reaching the nostril"; "toes pointed; web not extending to the tip of the first phalangeal bone, rather stopping at the base"; "inner metatarsal about ½ the diameter of the eye"; "upper surface of the skin slightly granulate, with short interrupted longitudinal folds with a few tubercles"; a ∩-shaped mark found on the back behind the shoulders; dorsum chocolate red.

We assign this new collection from the type locality as the neotype of *Rana (Hylorana) sauriceps* Rao, 1937, an action we consider necessary in accordance with Article 75 of The Code, owing to the following reasons: (1) The unavailability of its name bearing type (Dubois, 1984; Biju, 2001; present study) or any new referable material since the original description. (2) In the absence of a type, direct evidence on the holotype of *Rana (Hylorana) sauriceps* currently exists only from the original description and accompanying figure (Rao, 1937). However, the description by Rao (1937) is imprecise and not particularly informative. Several of the stated characters, particularly "Upper surface of the skin slightly granulate, with short interrupted longitudinal folds with a few tubercles" and "a ∩-shaped mark found on the back behind the shoulders", also overlap with other recognised and morphologically cryptic congeners, especially *M. brevipalmata* (Peters, 1871), *M. mysorensis* (Rao, 1920),

Table 1 Average uncorrected *p*-distances (in percentage) between *Minervarya* species for the mitochondrial 16S rRNA gene sequences.

M. sahyadris																										
M. gomantaki	4.9																									
M. krishnan	7.5	4.2																								
M. syhadrensis	6.3	8.2	10.1																							
M. nepalensis	6.8	9.5	11.7	2.6																						
M. pentali **sp. nov.**	8	9.4	11.1	5.2	7.1																					
M. greenii	9.3	10.7	12.7	7.8	9.1	9																				
M. kirtisinghei	9.2	10.6	12.2	6.7	8.6	7.9	4.1																			
M. asmati	8.7	8.2	8.8	9.5	9.8	9.8	9.2	9.3																		
M. chiangmaiensis	9.3	8.9	9.1	10.4	10.7	9.8	10.4	10.6	2.3																	
M. teraiensis	9.5	9.3	9.4	10.6	11	10.8	10.7	10.2	3.6	2.6																
M. mysorensis	8.9	10	12	8.4	9.3	8.3	9.3	9.2	8.6	9.3	9.6															
M. brevipalmata	8.7	9.9	11.4	8.2	9.1	9.7	6.8	6.7	7.5	9.1	10.1	5.1														
M. goemchi	8.4	9.6	11.8	7.9	8.2	8.8	7.3	7.4	7.3	8.2	9.2	3	2.7													
M. agricola	9.5	10.1	10.9	10.6	10.6	9.7	10.9	10.7	8.7	7.7	8.3	9.8	9.6	8.9												
M. andamanensis	11.6	12.9	15	10.4	11.1	11	11.1	11.6	11.5	12.1	13.6	10.9	10.4	10.2	12.3											
M. muangkanensis	11.7	12.8	15	9.5	10.7	11.1	10.7	10.9	11.5	12.4	12.3	10	10.4	10	10.6	5.2										
M. rufescens	12.2	14	15.1	12.1	12.6	12.8	9.8	10	12.1	13	13.2	11.5	11.5	11	14.1	12.4	10.8									
M. kadar	13	14.6	15.6	13	13.4	14.4	11.1	11.6	13.7	14.3	14.6	13.2	13	12.3	15.8	12.4	11.7	3.9								
M. manoharani	12.2	14	14.7	13	13.4	13.7	10.7	11.2	13.1	14	14.2	13.2	12.1	12.1	15.8	12.4	12.4	5.1	4.9							
M. neilcoxi	11.1	13.2	14.3	12.1	12.4	12	10.4	10.6	12.1	12.1	12.3	11.4	11.4	11.2	14.2	11.4	11.7	3.8	5.5	4.6						
M. cepfi	11.4	13.5	13.9	11.5	12.1	11.4	10.2	10.3	12.5	13.3	13.2	12.7	12.1	11.9	13.8	11.7	11.5	5.1	6.6	6.6	5.1					
M. marathi	10.6	12.1	14.3	10.4	11.7	11.3	9.8	9.6	10.2	11.4	12.4	11.4	10.7	10.5	11.9	9.4	10.7	8.9	10.7	9.4	8.8	10.1				
M. keralensis	12.6	13.4	15.6	11.1	11.7	11.1	10.7	10.9	12.4	12.4	14	12.5	10.7	11.2	11.9	11.4	13.4	14.4	15.3	14.3	13.4	13.9	10.7			
M. kalinga	13	12.9	15.1	11.7	12.4	12	11.1	10.9	11.8	12.4	13.3	11.3	10.6	9.8	13.2	11.7	13	13.2	15	14	13.4	13.3	11.4	7.3		
M. nilagirica	13.3	13.6	15.3	11.4	12.4	10.4	10.4	10.6	11.1	11.7	12	12.6	12.4	12.5	12.5	11.1	12.7	13.4	15	13.4	12.4	12	9.4	6.5	5.2	

and *M. kudremukhensis* (Kuramoto *et al.*, 2008 "2007"), some of which in addition have overlapping or close distribution ranges. (3) Moreover, the specific taxonomic status of *Rana (Hylorana) sauriceps* itself has been previously doubted with a proposal to consider it as *incertae sedis* in the genus *Fejervarya* (Dubois, 1987 "1986") that added to the confusion in assigning this nomen to any known living population ever since its original description. Hence, based on new evidence gathered in the present study, designation of a neotype is considered essential for defining this taxon objectively, in order to identify it properly from other close congeners, as well as to stabilise the taxonomic status of the nomen. We hereby designate BNHS 6114 from the original type locality "Wattekole" as the neotype of *Rana (Hylorana) sauriceps* Rao, 1937 (= *Minervarya sauriceps*). The neotype description provided below is largely consistent with what is known of the former name-bearing type.

Description of neotype of *Rana (Hylorana) sauriceps* Rao, 1937. By present designation, Neotype: BNHS 6114 (Figure 3), from "Wattakole" (Watekolli), Karnataka state, India, collected by S. D. Biju on 17 August 2013. A medium-sized adult male (SVL 40.5); head longer (HL 14.5) than wide (HW 13.2); snout sub-elliptical to pointed in dorsal and ventral view, obtuse in lateral view, its length (SL 6.4) longer than horizontal diameter of eye (EL 3.9); loreal region flared and concave with indistinct canthus rostralis; interorbital space narrower (IUE 2.3) than upper eyelid width (UEW 2.8) and internarial distance (IN 3.4); tympanum oval, its horizontal diameter (TYD 2.1) nearly half (53.8%) of the eye diameter (EL 3.9); forearm (FAL 6.3) shorter than hand length (HAL 8.7); outer, inner, and middle metacarpal tubercles present on hand, well developed; thigh (TL 18.7) shorter than shank (SHL 20.0) and foot (FOL 23.4); foot webbing small: I1– 2II1–2III1–3IV3–1V; inner metatarsal tubercle prominent (IMT 2.0), oval, raised; outer metatarsal tubercle small, rounded. Dorsal skin shagreened to sparsely granular with short longitudinal skin folds; a faint inverted "V"-shaped ridge on anterior half of the dorsum, at the level of forearms; lateral surfaces of head shagreened; flanks shagreened to sparsely granular; fore- and hind limbs shagreened with a few scattered tubercles. Ventral surfaces shagreened, and posterior surfaces of thighs granular. *Colour in preservation.* Dorsum light reddish-brown without any prominent markings; upper half of tympanum and inner margins of supratympanic fold light brown; flanks with faint blackish-brown patches; fore- and hind limbs without cross-bands; dorsal surfaces of posterior half of thigh light brown with buff-coloured reticulations. Ventral surfaces greyish-white with a yellow tinge.

Synonymisation of *Rana (Hylorana) sauriceps* Rao, 1937. We also compared the original description and our new collections of this taxon with all other known *Minervarya* species found in the Western Ghats. Evidence gathered from new morphological and molecular data finds *Rana (Hylorana) sauriceps* Rao, 1937 (= *Minervarya sauriceps*) to be conspecific with *M. mysorensis*. Most morphological characters (including adult size) were observed to be extremely similar or overlapping between these two currently recognised taxa, barring some minor intraspecific variations. Furthermore, mitochondrial 16S rRNA sequence data from the neotype specimen of *M. sauriceps* nested together with various populations of *M. mysorensis* (Figure 1) with maximum genetic distances of up to 1.0%, which fall within the range of intraspecific distances observed for the various *Minervarya* species in our study (Table 1). Hence, in accordance with the Article 23 (Principle of Priority) of The Code we consider *Rana (Hylorana) sauriceps* Rao, 1937 (= *Minervarya sauriceps*) as a junior subjective synonym of *Rana (Rana) limnocharis mysorensis* Rao, 1922 (= *Minervarya mysorensis*).

***Minervarya kudremukhensis* (Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007"): re-examination of taxonomic status and synonymy.** This taxon was originally described as *Fejervarya kudremukhensis* from "Kudremukh" based on a male holotype (Figure 3) and three paratypes, including a female specimen (Kuramoto *et al.*, 2008 "2007"). While describing this new species the authors compared and distinguished it mainly from four other known 'large-sized' members of the genus: *M. brevipalmata*, *M. keralensis*, *M. nilagirica*, and *M. mudduraja*. Of these, the last was described as a new species in the same study as *M. kudremukhensis* (Kuramoto *et al.*, 2008 "2007"), while for the former three members the authors clearly stated that they did not collect any specimens and solely relied on museum specimens for largely morphometric comparisons. However, the authors did not specifically compare their new taxon with *M. mysorensis*, *M. parambikulamana*, and *M. sauriceps*, assuming them to be smaller-sized species. Our extensive collections of minervaryan frogs from the Western Ghats show that various populations of *M. 'kudremukhensis'* (including the examined type series) share overlapping size ranges and several other similar morphological characters with these three species. For example, adult size range, dorsal skin with short longitudinal skin folds and an inverted "V"-shaped ridge, snout subelliptical to pointed, tympanum about half of the eye diameter, hind limbs relatively long, relatively reduced foot webbing not extending beyond the second subarticular tubercle on either side of toe IV, mottling on posterior surface of thighs, and most specimens showing the presence of a mid-dorsal vertebral line. Furthermore, since our study reports new collections of *M. mysorensis*, *M. parambikulamana*, and *M. sauriceps*, based on which their taxonomic identities have been clarified, there remains no doubt that *M. kudremukhensis* is conspecific with all of these taxa, and should hereafter be considered a junior subjective synonym of *M. mysorensis*, based

not only on morphological but also conclusive phylogenetic evidence (Figure 1). Hence, in accordance with the Article 23 (Principle of Priority) of The Code we consider *Fejervarya kudremukhensis* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007" (= *Minervarya kudremukhensis*) as a junior subjective synonym of *Rana (Rana) limnocharis mysorensis* (Rao, 1922) (= *Minervarya mysorensis*).

***Minervarya nilagirica* (Jerdon, 1853): taxonomic clarity and range extension.** This taxon was originally described as *Rana nilagirica* based on specimens from "marshes in the Wynaad and Neelgherries", with a brief description (Jerdon, 1853). However, the original name-bearing type of this nominal species was subsequently reported to be lost (Jerdon, 1870). Most subsequent authors considered this taxon either as a subspecies or junior synonym of *Fejervarya limnocharis* (e.g., Annandale, 1917; Boulenger, 1882, 1920). However, Dubois (1984) regarded it as a distinct species under his subgenus *Fejervarya* and designated a neotype (MNHNP 1984.2340) from "Governor Shola", Nilgiris, Tamil Nadu, India (Figure 3). Thereafter, the species was treated as a member of the genus *Fejervarya* sensu lato (e.g., Iskandar, 1998; Fei *et al*., 2002; Dinesh *et al*., 2015), until the recognition of the generic name *Minervarya* (sensu lato) for the predominantly South Asian radiation of what were formerly considered as fejervaryan frogs (Sanchez *et al*., 2018). However, despite its largely undoubted status as a distinct species as well as availability of a name-bearing type, *Minervarya nilagirica* is known only from the region of its original type locality. Our extensive collections of minervaryan frogs from the Western Ghats results in the following major findings: (1) significant extension of the geographical range of *Minervarya nilagirica* based on morphologically and genetically identified records from the Anaimalai hills (south of Palghat gap) to the hill ranges of Nilgiris, Siruvani, Wayanad, Coorg, and Chikmagalur, including Kempholey ghat, Shiradi ghat, and Kudremukh regions (north of Palghat gap), altogether encompassing the states of Tamil Nadu, Kerala, and Karnataka (Table S1; Figure 2); and (2) clarity on the identity and taxonomic status of two other nominal taxa from the Western Ghats—*Rana murthii* Pillai, 1979 (= *Minervarya murthii*) and *Fejervarya mudduraja* Kuramoto, Joshy, Kurabayashi, and Sumida 2008 "2007" (=*Minervarya mudduraja*)—both of which are shown to be junior subjective synonyms of *Minervarya nilagirica* (Jerdon, 1853), with formal actions of synonymy undertaken below in the subsequent sections.

***Minervarya murthii* (Pillai, 1979): re-examination of taxonomic status and synonymy.** This taxon was originally described as *Rana murthii* Pillai, 1979 based on three male (including holotype) and two female specimens from "Naduvattom", in the Nilgiris district of Tamil Nadu state. Pillai (1979) had discussed a single character to compare this species with *Fejervarya limnocharis* (referring to *Minervarya nilagirica*), *M. brevipalmata*, and *M. greenii*, i.e., "anterior part of lower jaw and two triangular patches on breast beset with small pearl-like papillae". However, an examination of the male holotype of *M. murthii* does not show "pearl-like papillae" on the breast or the lower jaw (Figure 3). Given that the holotype of *M. murthii* and the neotype of *M. nilagirica* cannot be distinguished based on this character, the distinct status of *M. murthii* becomes doubtful. We instead observed one of the male paratypes of *M. murthii* as having granulations on the chest and lower jaw, which were absent in the holotype and the other male paratype. Hence, the presence of 'pearl-like papillae' appears to be a variable character even in reproductively active males. In this context, Kuramoto *et al*.'s (2008 "2007") observation of "one exceptional individual" of *M. kudremukhensis* syn. nov. (= *M. mysorensis*) having "six faint longitudinal series of small dots on the throat and breast", suggests that this character could be found variably in other members of the genus *Minervarya*. In our study, we also observed discolouration on the chest with sparse granulation in a few breeding males of *M. nilagirica*. Ruling out this character, we do not find any other reliable morphological differences between these two taxa. Although the size of the respective type specimens vary (*M. murthii*, holotype, male: SVL 31.1 mm; *M. nilagirica*, neotype, male: SVL 43.4 mm), it is considered a sampling disparity as multiple collections from our study show considerable size variation and overlap among specimens from Naduvattam (male: SVL 32–42 mm, $N = 5$ and female: SVL 34–49 mm, $N = 5$) and Governor Shola (male: SVL 28–47 mm, $N = 4$ and female: SVL 38–51 mm, $N = 5$). In addition to the lack of morphological differentiation, the type localities of *M. murthii* "Naduvattam" and *M. nilagirica* "Governor Shola" lie in close proximity within the same geographical region (less than 20 km apart, with similar elevation and habitat), further suggesting these to be continuous populations of the same species. This is also congruent with molecular evidence presented in this study based on 16S mtDNA, which shows negligible genetic distance between these taxa. Hence, in accordance with the Article 23 (Principle of Priority) of The Code we consider *Rana murthii* Pillai, 1979 (= *Minervarya murthii*) as a junior subjective synonym of *Rana nilagirica* Jerdon, 1853 (= *Minervarya nilagirica*).

***Minervarya mudduraja* (Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007"): re-examination of taxonomic status and synonymy.** This taxon was originally described as *Fejervarya mudduraja* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007" based on four female specimens, of which the holotype (Figure 3) is from "Talapu, Madikeri" and the paratypes from close vicinities in Kodagu district of southern Karnataka. While recognizing this species, the

authors compared and distinguished it mainly from four other known 'large-sized' members of the genus: *M. brevipalmata*, *M. keralensis*, *M. nilagirica*, and *M. kudremukhensis*. As clarified under the discussion for *M. kudremukhensis*, the authors did not collect any specimens of the former three taxa and relied on museum specimens for morphometric comparisons, largely with respect to relative proportions of body parts. For example, *M. mudduraja* (females only) was distinguished from the closely related *M. nilagirica* by longer hind limbs, foot, and hand; from *M. keralensis* by relatively smaller head width, tympanum, and inner metatarsal tubercle; from *M. brevipalmata* also by relatively smaller inner metatarsal tubercle and relatively larger eyelid width compared to inter-orbital distance; and from *M. kudremukhensis* by longer hands, fingers, and toes. Among these species, our further detailed morphological and molecular study reveals *M. mudduraja* to be conspecific with *M. nilagirica*. Based on examination of seven males and four females from the type locality Madikeri and surrounding regions, along with the holotypes of *M. mudduraja* and *M. murthii*, and the neotype of *M. nilagirica*, we found that various quantitative and qualitative characters do not permit a reliable morphological distinction of the three species from one another. In addition, a genealogical comparison of our new 16S mtDNA data from topotypic collections of *M. nilagirica* and *M. murthii* from Governor shola and Naduvattam, respectively, with the previously available sequences of *M. mudduraja* originating from the type specimens, shows maximum genetic distances of up to 0.8%, which fall within the range of intraspecific distances observed among populations of the same species in the genus *Minervarya* (Table 1). Hence, in accordance with the Article 23 (Principle of Priority) of The Code we consider *Fejervarya mudduraja* Kuramoto, Joshy, Kurabayashi, and Sumida, 2008 "2007" (= *Minervarya mudduraja*) as a junior subjective synonym of *Rana nilagirica* Jerdon, 1853 (= *Minervarya nilagirica*).

***Minervarya modesta* (Rao, 1920): re-examination of taxonomic status and synonymy.** Another poorly known species, *Minervarya modesta*, was originally described as *Nyctibatrachus sanctipalustris* var. *modestus* Rao, 1920 based on a holotype from "Jog, Shimoga, Mysore". New specimens of this species have not been recorded ever since its original description. Biju *et al.* (2011) reviewed this taxon, discussed its taxonomic history, and formally transferred it to the genus *Fejervarya* (sensu lato) based on examination of the available holotype. In the present study, we collected several individuals of a *Minervarya* species from Mavinagundi (near Jog falls) in Uttara Kannada district and Shimoga in Shimoga district of Karnataka state. Although the original description of *Nyctibatrachus sanctipalustris* var. *modestus* Rao, 1920 is brief, ambiguous, and mostly includes a comparison with the originally assigned species, in addition to the holotype (ZSIC 19179) being severally damaged, we found our new collections to largely match with the available name-bearning type and some of the described characters, chiefly with respect to the adult snout-vent size (SVL 23.1 mm) and dorsal skin with "long longitudinal folds on the body and limbs". Furthermore, our newly generated 16S mtDNA sequence from a topotypic specimen (SDBDU 2017.3677) nests together with various studied populations of *M. sahyadrensis* with negligible to maximum 0.8% intraspecific divergence. Hence, we propose *Nyctibatrachus sanctipalustris* var. *modestus* Rao, 1920 (= *Minervarya modesta*) to be considered as a junior subjective synonym of *Minervarya sahyadrensis* (Annandale, 1919).

***Minervarya jhilmilensis* (Bahuguna, 2018): re-evaluation of generic placement.** Although this study focused on *Minervarya* frogs of the Western Ghats, we sampled some populations of species with geographical ranges extending outside the region. During our surveys, we encountered a population morphologically identical to *Fejervarya jhilmilensis* (= *Minervarya jhilmilensis*) (Sanchez *et al.*, 2018) at Haridwar, in close proximity to its type locality. This species was genetically close to members of the genus *Fejervarya* rather than members of the genus *Minervarya*, with zero to maximum genetic distances of up to 2.5% from *F. 'orissaensis'* for the mitochondrial 16S gene sequences. Therefore, the species is removed from the genus *Minervarya* and formally placed in the genus *Fejervarya*. However, we defer the evaluation of the specific taxonomic status of *Fejervarya jhilmilensis* for a future study of fejervaryan frogs.

3.3. Description of a new species

***Minervarya pentali* sp. nov.**

Pental's Minervaryan Frog

(Tables 1–2; Figures 1–2, 4)

Etymology: The species is named after Prof. Deepak Pental, a renowned Indian Plant Genetist and former Vice Chancellor of University of Delhi, in appreciation of his contributions to science. We also acknowledge his support and encouragement in setting-up of the Systematics Lab at Department of Environmental Studies, University of Delhi. The species epithet *pentali* is treated as a noun in the genitive case.

Holotype: BNHS 6115, an adult male, from Nedumbassery, Cochin (10°09'42.5" N 76°23'22.4" E, 11 m asl), Ernakulam district, Kerala state, India, collected by S. D. Biju and Sonali Garg on 29 July 2014.

Paratypes: BNHS 6116–BNHS 6119, four adult males, from Nedumbassery, Cochin (10°09'42.5" N 76°23'22.4" E, 11 m asl), Ernakulam district, collected along with the holotype.

Referred specimen: SDBDU 2017.3628, an adult female from Kuriyode, Kollam district, Kerala state, collected by Sonali Garg

Table 2 Morphometric measurements for the type series and referred specimen of *Minervarya pentali* **sp. nov.** (in mm).

	BNHS 6115 (HT) ♂	BNHS 6116 (PT) ♂	BNHS 6117 (PT) ♂	BNHS 6118 (PT) ♂	BNHS 6119 (PT) ♂	Range	Mean ±S.D.	SDBDU 2017.3628 (RS) ♀
SVL	19.3	22.5	20.7	22.4	20.6	19.3–22.4	21.1±1.4	26
HW	5.9	6.4	6.5	6.6	6.2	5.9–6.6	6.3±0.3	8.9
HL	8.1	8	8.1	8.4	8.2	8.0–8.4	8.2±0.2	10.3
TYD	1.2	1.3	1.2	1.4	1.2	1.2–1.4	1.3±0.1	1.7
SL	3.1	3.4	3.2	3.5	3.3	3.1–3.5	3.3±0.2	4.2
EL	2.2	2.2	2.4	2.5	2.1	2.1–2.5	2.3±0.2	2.7
IUE	1.6	1.8	1.6	1.9	1.5	1.5–1.9	1.7±0.2	2.3
UEW	1.5	1.7	1.8	1.8	1.7	1.4–1.5	1.7±0.1	2.3
EN	1.2	1.5	1.4	1.5	1.4	1.2–1.5	1.4±0.1	2.4
NS	1.2	1.3	1.4	1.4	1.5	1.2–1.5	1.4±0.1	1.3
IN	1.7	1.8	1.9	1.9	1.8	1.7–1.9	1.8±0.1	2
FAL	3.4	3.7	3.8	4.2	3.5	3.4–4.2	3.7±0.3	5
HAL	4.6	4.9	4.9	5.1	4.7	4.6–5.1	4.8±0.2	6.6
TL	8.2	8.4	8.3	8.7	8	8.0–8.7	8.3±0.3	11.8
SHL	8.9	9.5	9.4	9.7	9.5	8.9–9.7	9.4±0.3	13.1
FOL	9	9.7	9.6	9.8	9.5	9.0–9.8	9.5±0.3	13.3
TFOL	13.9	14.9	14.1	14.9	14.1	13.9–14.9	14.4±0.5	20.9

and S. D. Biju on 1 August 2017.

Description of holotype: A small-sized adult male (SVL 19.3 mm), body rather slender; head longer (HL 8.1 mm) than wide (HW 5.9 mm; MN 6.2 mm; MFE 5.0 mm; MBE 3.1 mm); snout shape sub-elliptical in dorsal view, rounded in lateral view, slightly protruding, snout length (SL 3.1 mm) longer than horizontal diameter of eye (EL 2.2 mm); loreal region acute, rounded canthus rostralis; interorbital space flat, nearly equal to (IUE 1.6 mm) upper eyelid width (UEW 1.5 mm) and sub-equal to internarial distance (IN 1.7 mm); nostril oval, as close to the tip of snout (NS 1.2 mm) as to the eye (EN 1.2 mm); tympanum (TYD 1.2 mm) 54.5% of eye diameter (EL 2.2 mm); tympanum to eye distance (TYE 0.7 mm) 58.3% of the tympanum diameter; pineal ocellus present; supratympanic fold well developed, extends from posterior corner of the eye to near the shoulder; vomerine ridge present, bearing small teeth, at an angle of 45° to the body axis, as close to choanae as to each other; tongue moderately long, emarginated (Figure 4).

Arms short, forearm length (FAL 3.4 mm) shorter than hand length (HAL 4.6 mm); fingers rather long, relative length of fingers II<I=IV<III (FL_I 2.1, FL_{II} 2.0, FL_{III} 2.6, FL_{IV} 2.1); tip of fingers bluntly rounded, not enlarged into discs; fingers without dermal fringe; webbing absent; subarticular tubercles prominent, single, circular, all present; prepollex oval, prominent; two rounded palmar tubercles; supernumerary tubercles absent.

Hind limbs short, thigh (TL 8.2 mm) shorter than shank (SHL 8.9 mm) and foot (FOL 9.0 mm), distance from the base of tarsus to the tip of toe IV (TFOL 13.9 mm); toes long, relative length of toes I<II<V<III<IV; toe tips rounded, slightly enlarged without discs, toes without dermal fringes, webbing between toes small: I1½–2II1½–2½III2–3IV3–1½V; subarticular tubercles prominent, all present, circular; inner metatarsal tubercle prominent (IMT 0.8 mm), cylindrical; outer metatarsal small (OMT 0.3 mm), rounded; supernumerary tubercles absent; inner tarsal ridge present.

Skin of dorsum shagreened with scattered glandular projections and short longitudinal glandular folds; an interrupted inverse V-shaped ridge at the centre of dorsum; snout shagreened, upper eyelids sparsely tuberculate; upper and lower parts of flank shagreened with a few granular projections. Dorsal surfaces of forelimb, thigh, and shank shagreened with sparsely glandular projections. Ventral surfaces of throat, chest, belly, and limbs smooth; and posterior parts of thigh and region surrounding the vent sparsely granular; fejervaryan lines present on both sides of the belly; rictal glands present, just behind the labial commissure of the mouth (Figure 4).

Colour in life. Dorsum greyish-brown with blackish-brown lining on skin folds; lateral surfaces of head lighter than dorsum (Figure 4); upper and lower lip with prominent crossbands, greyish-brown alternating with light grey; mid-dorsal line light yellowish-grey; rictal gland creamy white; anterior parts of flank light greyish-brown, forelimbs and hind limbs (including toes) lighter greyish-brown compared to the dorsum; limbs with dark greyish-brown transverse bands; groin greyish-yellow; anterior parts of thigh brown with yellowish-grey reticulations; webbing light grey. Ventral surface of throat flesh colour with a black calling patch; belly white; forearm and foreleg light flesh white with dark brown mottling on the margins. *Colour in preservation (alcohol)*. Dorsum brownish-grey, a thin creamy white mid-dorsal line extending from snout to the vent, a greyish-brown stripe between the eyes that extends over the upper eyelids; upper and lower jaw margins

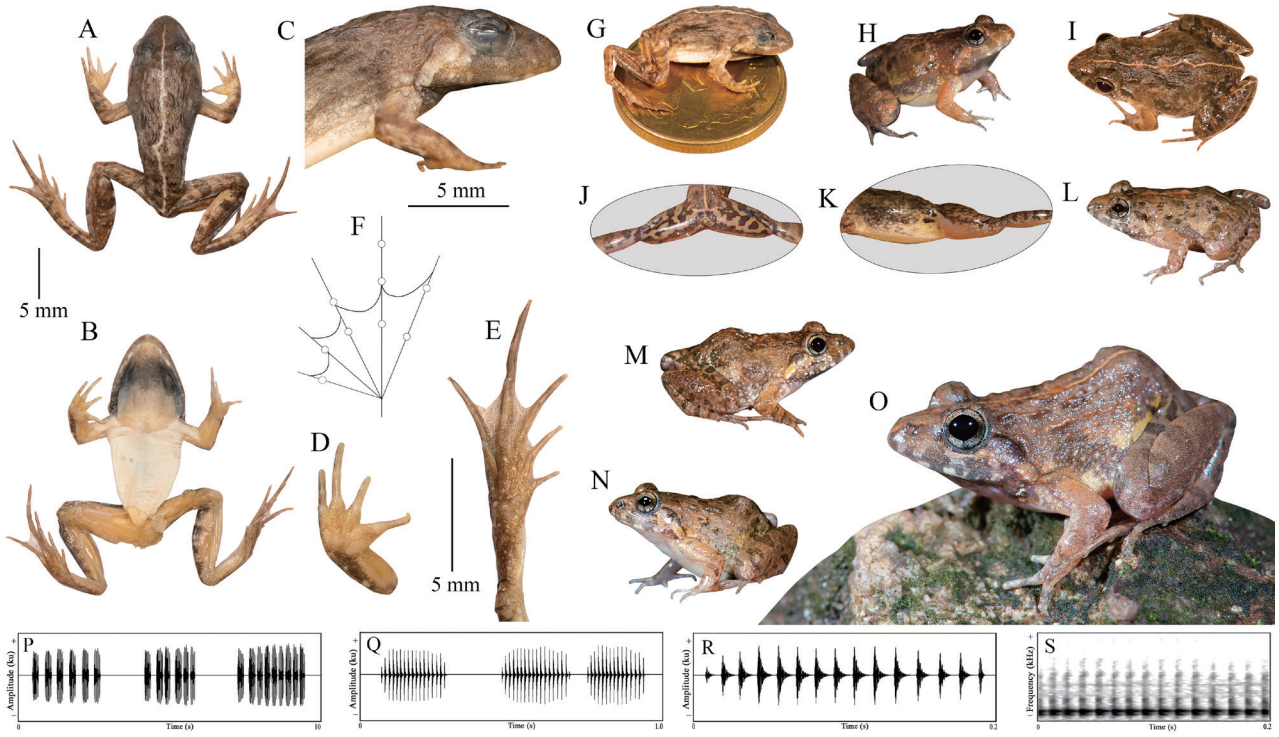

Figure 4 (A–G) Holotype of *Minervarya pentali* **sp. nov.** in preservation showing (A) dorsal view; (B) ventral view; (C) lateral view of head; (D) ventral view of hand; (E) ventral view of foot; (F) schematic illustration of foot webbing; (G) Size (SVL 19.3 mm) in comparison to the Indian five-rupee coin (23 mm diameter); (H–O) *Minervarya pentali* **sp. nov.** in life; (H–K) holotype showing (H) dorsolateral view; (I) dorsal view; (J) posterior view of thighs; (K) lateral view of groin; (L) paratype showing dorsolateral view; (M) paratype showing dorsolateral view; (N) paratype showing dorsolateral view; (O) paratype showing dorsolateral view; (P–S) male advertisement calls of *Minervarya pentali* **sp. nov.** showing (P) 10 second call segment with a single call type; (Q) 1 second call segment; (R) 0.2 second call segment; (S) spectrogram of the 0.2 second call segment shown in Figure 4R.

with faint light brown crossbands alternating with light grey; forelimbs and hind limbs lighter brown in colour than dorsum, with dark grey transverse bands; posterior parts of thigh light brown with dark brown reticulations. Ventral surface of throat with a dark grey to blackish calling patch; belly off-white; limbs light greyish-brown, with dark greyish-brown mottling on the margins; hand and foot light greyish-brown (Figure 4).

Morphological variation: Morphometric data from five adult males and one adult female, including the holotype, is given in Table 2. *In preservation*: BNHS 6116, BNHS 6118, and BNHS 6119: absence of a mid-dorsal line, and dorsal skin with relatively more granulations and skin folds; BNHS 6117: limbs relatively more granular; and SDBDU 2017.3628 (female): presence of a faint and thin mid-dorsal line, prominent dorsal skin folds and granulation, and loreal region nearly obtuse.

Secondary sexual characters: *Male* (HT). Nuptial pad on finger I present, one single patch on prepollex and finger I up to half the length of the penultimate phalange. Vocal sacs present, marked by loose blackish skin on throat. *Female* (SDBDU 2017.3628). Gravid with mature ova, pigmented on poles, diameter 0.6–0.7 mm (N = 30).

Morphological diagnosis: *Minervarya pentali* **sp. nov.** can be distinguished from other congeners by the following combination of morphological characters: (1) small adult size (male SVL 19–22 mm, N = 5; female SVL 24–26 mm, N = 2); (2) slender body; (3) snout shape sub-elliptical in dorsal view and rounded in lateral view; (4) presence of vomerine teeth; (5) finger and toe tips rounded, not enlarged into discs, without grooves; (6) dorsal skin sparsely granular with short discontinuous longitudinal skin folds; (7) presence of fejervaryan lines; (8) presence of rictal glands at labial commissure of the mouth; (9) eye length shorter than snout length (male EL/SL ratio 0.64–0.75, N = 5); (10) inter upper eyelid width narrower or nearly equal to upper eyelid width (male IUE/UEW ratio 0.88–1.06, N = 5); and inter upper eyelid width shorter or equal to internarial distance (male IUE/IN ratio 0.83–1, N = 5); (11) shank length nearly equal to foot length (male SHL/FOL ratio 0.98–1, N = 5); (12) foot webbing small; (13) absence of a white band along the upper lip margin; (14) first finger length equal or sub-equal to

the second finger length; (15) nostril nearly equidistant from the snout and eye (male EN/NS ratio 0.93–1.02, *N* = 5); (16) shorter hind limbs in comparison to the body length with tibio-tarsal articulation reaching up to the axilla when hind limb is stretched along the body.

Morphological comparison: *Minervarya pentali* **sp. nov.** cannot be confused with other known members of the genus *Minervarya* due to its small adult male body size, SVL ≤ 22 mm (*vs.* SVL > 25 mm), except four members of the *Minervarya sahyadris* group (*M. chilapata*, *M. gomantaki*, *M. krishnan*, and *M. sahyadris*). It differs from all the members of *Minervarya sahyadris* group in having granular dorsal skin with discontinuous longitudinal skin folds (*vs.* shagreened to sparsely granular, without or with weakly developed longitudinal skin folds); absence of white band along the upper lip margin (*vs.* upper lip with white horizontal band in all the four species); and relatively more foot webbing that extends well above the first subarticular tubercle on the outer side of toes I and II, and above the second subarticular tubercle on inner side of toe V (*vs.* relatively less, up to or below).

Within the *Minervarya syhadrensis* group, the new species resembles the morphologically and geographically close *M. syhadrensis*; however *Minervarya pentali* **sp. nov.** differs from the former by its smaller adult size, male SVL 19–22 mm, *N* = 5; female SVL 26 mm, *N* = 1 (*vs.* larger, male SVL 25–32 mm, *N* = 6; female SVL 34–41 mm, *N* = 3); snout sub-elliptical in dorsal view (*vs.* nearly pointed); shank nearly equal to foot length, male SHL/FOL ratio 0.98–1, *N* = 5, female SHL/FOL ratio 0.98, *N* = 1 (*vs.* shank shorter than foot, male SHL/FOL ratio 0.89–0.92, *N* = 6, female SHL/FOL ratio 0.96, *N* = 1); small foot webbing, I1½–2II1½–2½III2–3IV3–1½V (*vs.* moderate, $I1^{+}$–$2II1^{+}$–$2^{-}III1^{+}$–$3^{-}IV3^{-}$–$1^{+}V$); and short discontinuous dorsal skin folds in fewer rows (*vs.* relatively more prominent and longer longitudinal skin folds in more rows). *Minervarya pentali* **sp. nov.** differs from another known member of the group from Nepal, *M. nepalensis* (based on the type series), by its smaller adult size, male SVL 19–22 mm, *N* = 5; female SVL 26 mm, *N* = 1 (*vs.* larger, male SVL 29–35 mm, *N* = 8; female SVL 30–45 mm, *N* = 12); and small foot webbing, below the second subarticular tubercle on either side of toe IV, I1½–2II1½–2½III2–3IV3–1½V (*vs.* moderate, up to third subarticular tubercle on either side of toe IV, $I1^{-}$–$2^{-}II1^{+}$–$2III1^{+}$–$2IV2$–$1^{+}V$).

Although the new species is distinguishable from all other known members of the genus by its small size, in order to avoid confusion, specific comparison is provided with all other known members by their respective species groups. *Minervarya pentali* **sp. nov.** differs from members of the *M. agricola* group by its smaller adult size, male SVL ≤ 22 mm (*vs.* male SVL 22–41 mm), and smaller foot webbing that does not extend beyond the second subarticular tubercle on either side of toe IV (*vs.* above); differs from members of the *M. andamanensis* group by its smaller adult male size, SVL ≤ 22 mm (*vs.* male SVL 33–47 mm), relatively more granular dorsal skin with longitudinal skin folds (*vs.* less granulations and weakly developed or absence of skin folds), and smaller foot webbing that does not extend beyond the second subarticular tubercle on either side of toe IV (*vs.* above); differs from members of the *M. greenii* group by its smaller adult male size, SVL ≤ 22 mm (*vs.* male SVL 25–41 mm), and smaller foot webbing that does not extend beyond the second subarticular tubercle on either side of toe IV (*vs.* above); differs from members of the *M. mysorensis* group by its smaller adult male size, SVL ≤ 22 mm (*vs.* male SVL 35–53 mm), and shorter hind limbs in comparison to the body length with tibio-tarsal articulation reaching up to the axilla when hind limb is stretched along the body (*vs.* longer hind limbs with tibio-tarsal articulation reaching up to the snout); differs from members of the *M. nilagirica* group by its smaller adult male size, SVL ≤ 22 mm (*vs.* male SVL 32–46 mm), small foot webbing that does not extend beyond the second subarticular tubercle on either side of toe IV (*vs.* above), and thighs light brown with light yellowish-grey reticulations (*vs.* dark blackish-brown with prominent and contrasting golden yellow reticulations); and differs from members of the *M. rufescens* group by its smaller adult male size, SVL ≤ 22 mm (*vs.* male SVL 24–35 mm), slender body (*vs.* stout body), head longer than wide (*vs.* head wider than long or sub-equal), short and cylindrical inner metatarsal tubercles (*vs.* shovel-shaped), and dorsal skin with longitudinal skin folds (*vs.* without longitudinal skin folds). Further, *Minervarya pentali* **sp. nov.** differs from *M. marathi*, provisionally considered a member of the *M. andamanensis* group, by its smaller adult size, male SVL 19–22 mm, *N* = 5, female SVL 26 mm, *N* = 1 (*vs.* larger, male SVL 34–44 mm, *N* = 4, female SVL 41–49 mm, *N* = 6).

Phylogenetic relationship: *Minervarya pentali* **sp. nov.** is a well-supported distinct lineage and member of the *Minervarya syhadrensis* group (Figure 1). At the mitochondrial 16S locus, it is divergent from other members of the group by average uncorrected pairwise genetic distances of: 4.9% (range 4.7%–4.9%) from *M. nepalensis*; and 4.4% (range 4.0%–5.1%) from *M. syhadrensis*.

Vocalisation: The male calls of *Minervarya pentali* **sp. nov.** were recorded at Nedumbassery on 29 July 2014, between 20:00–21:00 h, in ambient air temperature: 25.0°C dry bulb, 24.0°C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. A typical call was 223.1 ms long in duration; showed a rise time of 35.2 ms and fall time of 22.1 ms; with the call envelope comprising 19 pulses delivered at a rate of 83.6 pulses/second. The call spectrum was characterised by two broad peaks with mean dominant frequency of 3.1 kHz

(Figure 4).

Distribution and natural history: *Minervarya pentali* **sp. nov.** is endemic to the southern Western Ghats, where it is currently known to be widely distributed in the low-lying regions, from sea level up to the elevations of 220 m asl, nearly across the entire state of Kerala and the adjoining areas of Tamil Nadu. Kerala state: Thiruvananthapuram district (Chathankod and Karamana), Kollam district (Kuriyode and Nilamel), Pathanamthitta district (Kulanada), Alappuhza district (Alleppy and Karthikappally), Ernakulam district (Angamally and Nedumbaserry), Thrissur district (Thrissur town), Malappuram district (Thenjipalam and Kadakkattupara), and Kozhikode district (Calicut city and suburban areas, and Ramanattukara); Tamil Nadu state: Kanyakumari district: Kiriparai (Figure 2). The species presumably has a wider distribution within its known range in Kerala and adjoining lowland regions of Tamil Nadu. In the present study, the species was predominantly observed in wayside vegetated areas close to permanent water bodies or temporary water collection sites, agricultural fields, and small-scale plantations within human settlements, but not inside forested areas. During the breeding season (July to September) males aggregate in large numbers on the ground, among grasses, or vegetation edges, near water bodies and temporary puddles. Calling activities have been recorded between 18:00–22:00 hours.

3.4. Grouping of species in the genus *Minervarya* Species belonging to the genus *Minervarya* can be assigned to eight distinguishable groups, primarily adapted from Garg and Biju (2017) and expanded herein based on further evidence. Although the revised scheme of grouping presented below is defined using morphological traits, most groups also find support in our preliminary phylogenetic analyses (Figures 1, 5 and 6). In the future, robust multi-locus phylogenies and phenotypic traits such as acoustics and behavior can be used to provide additional evidence as well as diagnostic characters for these species-groups, which are proposed with the aim of facilitating a better working taxonomy for this group of morphologically confusing frogs.

***Minervarya agricola* group**

Members included: *Minervarya agricola*, *M. asmati*, *M. chiangmaiensis*, *M. teraiensis*, and *M. sengupti*. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: small to medium adult size (male SVL 20–47 mm, female SVL 27–54 mm); elongate to robust body; head longer than wide; moderate foot webbing, beyond the second subarticular tubercle on either side of toe IV; long and cylindrical inner metatarsal tubercles; dorsal skin with short discontinuous skin folds, with or without scattered granular projections; dorsal chevron present; groin without prominent markings or reticulations; thigh with faint reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya agricola* group is closely related to the *Minervarya sahyadris* and *Minervarya syhadrensis* groups (Figure 1). **Distribution:** India, Sri Lanka, Bhutan, Nepal, Bangladesh, Myanmar, Thailand, up to southern China (Figure 2).

***Minervarya andamanensis* group**

Members included: *Minervarya andamanensis* and *M. muangkanensis*, and provisionally *M. marathi* and *M. nicobariensis*. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: medium adult size (male SVL 33–47 mm, female SVL 40–54 mm); elongate to robust body; head longer than wide or sub-equal; moderate foot webbing, up to or above the second subarticular tubercle on either side of toe IV, and below the second subarticular tubercle on the inside of toe III; long and cylindrical inner metatarsal tubercles; dorsum shagreened to sparsely granular, with weakly developed short discontinuous skin folds; groin without prominent reticulations; thighs with faint reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya andamanensis* group shows a poorly resolved sister-group relationship with members of the *Minervarya rufescens* group and *M. marathi* (Figure 1). **Distribution:** India (Andaman and Nicobar Archipelago and northern Western Ghats), Myanmar, and Thailand (Figure 2).

***Minervarya greenii* group**

Members included: *Minervarya greenii* and *M. kirtisinghei*. **Morphological definition:** Medium adult size (male SVL 25–41 mm, female SVL 32–50 mm); elongate to robust body; head longer than wide; first finger longer then second finger; moderate foot webbing, above the second subarticular tubercle on either side of toe IV and below the second subarticular tubercle on the inside of toe III; long and cylindrical inner metatarsal tubercles; dorsum sparsely to prominently granular with long longitudinal skin folds; posterior surface of thighs with faint reticulations (Figures 5 and 6). **Phylogenetic relationship:** This group is provisionally proposed to accommodate two species currently known only from Sri Lanka, which are together recovered as a monophyletic group showing a distinct phylogenetic position within the genus based on the mitochondrial 16S locus, however with inconsistent group-level relationships (e.g., Dinesh *et al.*, 2015; Köhler *et al.*, 2019; Kotaki *et al.*, 2010; Phuge *et al.*, 2019; Raj *et al.*, 2018; Sanchez *et al.*, 2018; Sumida *et al.*, 2007; present study, Figure 1). **Distribution:** Endemic to Sri Lanka (Figure 2).

***Minervarya mysorensis* group**

Members included: *Minervarya brevipalmata*, *M. goemchi*, and

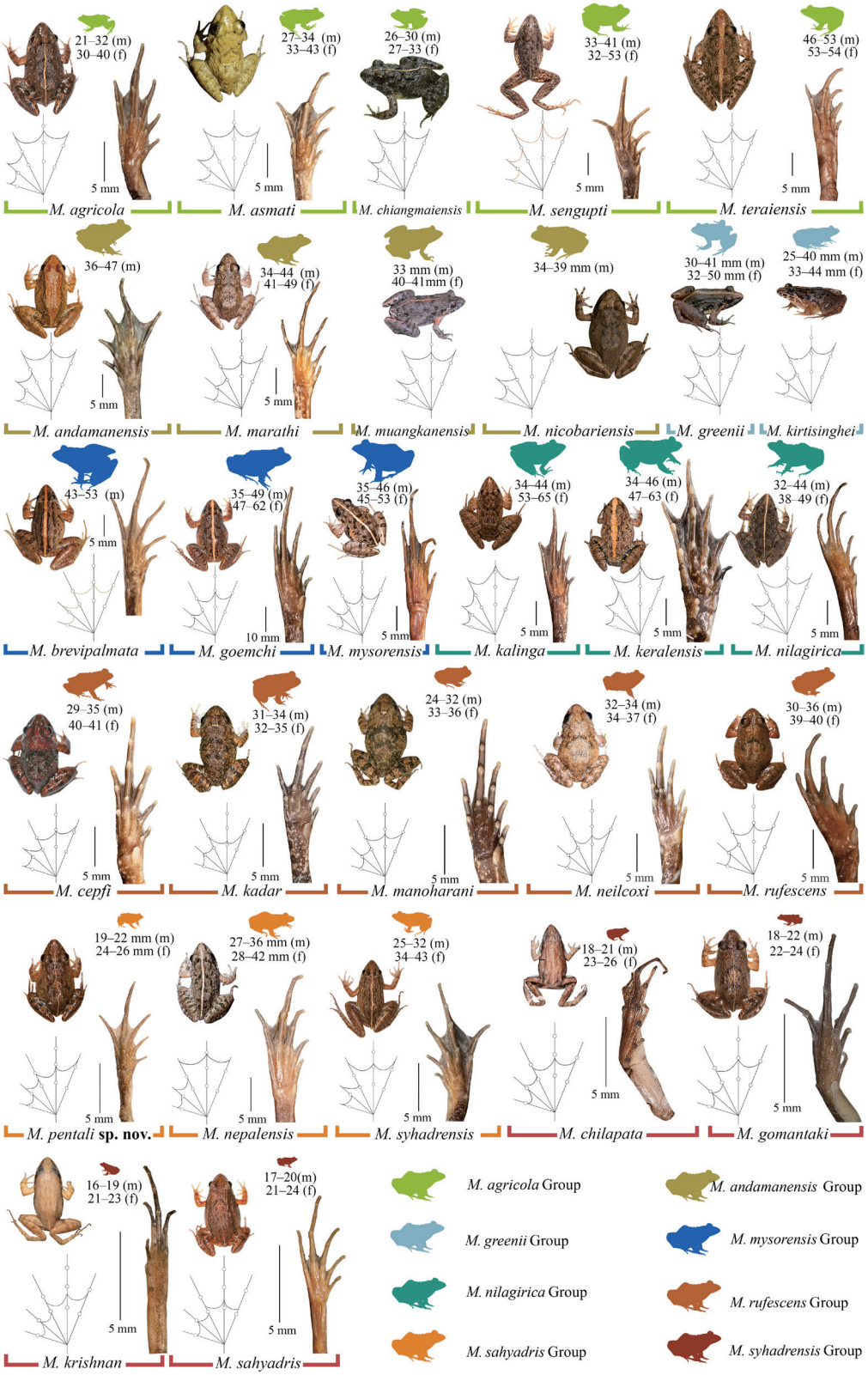

Figure 5 Morphological characters (clock-wise: dorsal skin texture; ventral surface of foot showing the extent of webbing, and inner and our metatarsal tubercles; and schematic illustration of foot webbing) for twenty-nine recognised *Minervarya* species, arranged in eight species groups identified in the study. Frog silhouettes for each species indicate the species group by colour and the proportionate adult snout-vent size (SVL) in millimeters.

Figure 6 Twenty-nine recognised *Minervarya* species depicted in life. Species are arranged in eight species groups identified in the study.

M. mysorensis. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: medium to large adult size (male SVL 35–54 mm, female SVL 45–65 mm); elongate or robust body; head longer than wide; small foot webbing, below or up to the second subarticular tubercle on either side of toe IV, below or up to the first subarticular tubercle on the outer side of toe III, and below or up to the second subarticular tubercle on the inner side of toe V; long and cylindrical inner metatarsal tubercles; dorsal skin with prominent folds, either continuous or discontinuous, and scattered granular projections; dorsal chevron present; groin without prominent reticulations; posterior surfaces of thigh with reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya mysorensis* group forms a well-supported monophyletic clade, however with weak to moderate support for group level relationships (Figure 1). **Distribution:** Endemic to the Western Ghats (Figure 2).

***Minervarya nilagirica* group**

Members included: *Minervarya kalinga, M. keralensis*, and *M. nilagirica*. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: medium to large adult size (male SVL 32–46 mm, female SVL 38–65 mm); robust body; head longer than wide or sub-equal; first finger longer than second finger

(except in *M. nilagirica*); moderate to large foot webbing, up to or above the second subarticular tubercle on either side of toe IV in *M. nilagirica*, and up to or above the third subarticular tubercle on either side of toe IV in *M. kalinga* and *M. keralensis*; long and cylindrical inner metatarsal tubercles; dorsal skin with prominent discontinuous folds, and glandular warts or prominent granulations; dorsal chevron present; groin and thighs with prominent reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya nilagirica* group is the most distinct group showing a well-supported sister-group relationship with all the remaining *Minervarya* species studied in a phylogenetic framework so far (Figure 1). **Distribution:** Endemic to Peninsular India both in the Western and Eastern Ghats (Figure 2).

***Minervarya rufescens* group**

Members included: *Minervarya cepfi*, *M. kadar*, *M. manoharani*, *M. neilcoxi*, and *M. rufescens*. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: small to medium adult size (male SVL 24–35 mm, female SVL 32–41 mm); stout body; head wider than long or sub-equal; presence of rictal glands at labial commissures of the mouth; small foot webbing, below the second subarticular tubercle on either side of toe IV; shovel-shaped inner metatarsal tubercles; dorsal skin with glandular projections, spines or warts, but without longitudinal skin folds; dorsal chevron present; groin without prominent reticulations; thighs with faint reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya rufescens* group shows a well-supported sequential sister relationship with *M. marathi* and members of the *Minervarya andamanensis* group (present study, Figure 1; Phuge *et al*., 2019; Sanchez *et al*., 2018). **Distribution:** Endemic to the Western Ghats (Figure 2).

***Minervarya syhadrensis* group**

Members included: *Minervarya pentali* **sp. nov.**, *M. nepalensis*, and *M. syhadrensis*. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: small to medium adult size (male SVL 19–35 mm, female SVL 23–45 mm); elongate body; head longer than wide; moderate foot webbing, up to the third subarticular tubercle on either side of toe IV; long and cylindrical inner metatarsal tubercles; dorsal skin with continuous or discontinuous skin folds, with or without scattered granular projections; dorsal chevron present; groin without reticulations; thighs with faint reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya syhadrensis* group is closely related to *Minervarya agricola* and *Minervarya sahyadris* groups (Figure 1). **Distribution:** Peninsular and Central India, and Nepal (Figure 2).

***Minervarya sahyadris* group**

Members included: *Minervarya chilapata*, *M. gomantaki*, *M. krishnan*, and *M. sahyadris*. **Morphological definition:** This group can be distinguished from other minervaryan groups by the following suite of characters: small adult size (male SVL 12–22 mm, female SVL 23–24 mm); slender body; head longer than wide; small foot webbing, up to or below the second subarticular tubercle on either side of toe IV; presence of rictal glands at labial commissures of the mouth and a white horizontal band along the upper lip; long and cylindrical inner metatarsal tubercles; dorsal skin with weakly developed longitudinal skin folds or granulations; dorsal chevron absent; groin without reticulations; thighs with faint reticulations (Figures 5 and 6). **Phylogenetic relationship:** Based on the 16S rRNA locus, the *Minervarya sahyadris* group is closely related to *Minervarya agricola* and *Minervarya syhadrensis* groups (Figure 1). **Distribution:** Currently a disjunct distribution in Peninsular India and Northeast India (Figure 2).

4. Discussion

Frogs of the genus *Minervarya* constitute a long-standing taxonomic enigma, especially because several species originally described from the Western Ghats had either not been reported ever since their original description or remained poorly known due to lack of new collections. In this study, we resolve numerous uncertainties regarding the identity as well as taxonomic status of ten nominal taxa, along with revisiting all of the 18 presently recognised members of the genus from Peninsular India, based on extensive sampling combined with comprehensive morphological and molecular studies. As a result, our study recognises 29 *Minervarya* species as valid, in contrast to the previously 35 known species (Frost, 2021; Khatiwada *et al*., 2021). The primary aim of our study was to resolve a taxonomic conundrum that had long deterred comprehensive and meaningful studies on this group of morphologically confusing frogs. In turn, our results also facilitate a better understanding of morphological characters useful for diagnosis of species and species-groups in the genus, systematic relationships among all known species, and extended geographical ranges, in addition to description of a new species.

Our extensive sampling and DNA barcoding of *Minervarya* frogs from regions across the Western Ghats also provide clarifications and significant extensions to the geographical ranges previously known for all Peninsular Indian species. The insights gathered on the patterns of distribution and endemism, will help future researchers in proper identification and better range delineation, especially considering the morphologically conserved and cryptic nature of species in the genus. The range

of the entire genus is also better understood after this study and can aid future phylogenetic and biogeographical studies, not only in relation to all of minervaryan frogs but also the closely related genera *Fejervarya* and *Sphaerotheca*. The genus *Fejervarya*, with which minervaryan species still continue to be confused—largely due to the overall conserved morphology, extended and overlapping geographical ranges outside of their major centres of diversity in South (*Minervarya*) and Southeast Asia (*Fejervarya*), and unresolved phylogenies (Dinesh *et al.*, 2015; Sanchez *et al.*, 2018)—is also confirmed to be distributed up to North India based on the transfer of *Minervarya jhilmilensis* to *Fejervarya*, and the recent reports of fejervaryan members from Nepal (Khatiwada *et al.*, 2021). Nonetheless, future studies are still essential to delineate the boundaries of these two genera and the factors possibly contributing to their broadly restricted geographical distributions.

Our study also indicates the presence of previously unknown cryptic diversity within the genus. Although the current evidence does not support recognition of putative new taxa delimited in the *Minervarya sahyadris* and *Minervarya agricola* groups (Figure 1), new insights are certainly likely to be gained from the observed population clusters. For example, members of the *Minervarya sahyadris* group are geographically restricted and appear to have narrower ranges. On the other hand, the *Minervarya agricola* group represents the most wide-ranging radiation within the genus, especially its namesake species *Minervarya agricola* that based on our sampling is known to occur right from the southern tip of the Indian Peninsula up to central, north, and east India. The high intraspecific distances observed among various populations of this taxon also suggest it to be a species complex that can prove to be a good model for understanding the patterns of genetic and possibly phenotypic differentiation, diversification, and distribution in minervaryan frogs. Such studies will also require proper evaluation of the taxonomic status and ranges of several other available names from Northeast India, Nepal, and the neighbouring Southeast Asia. Even within the Western Ghats, with the taxonomy of several species having been resolved, future surveys and detailed studies are likely to yield more undescribed taxa.

Hence, in order to facilitate a better working taxonomy for minervaryan frogs, and to eventually enable a much more comprehensive understanding of the genus across its entire range in South, Southeast, and East Asia, we recognise and redefine eight species-groups to accommodate all of the currently known *Minervarya* species. In the future, additional morphological data and robust phylogenies based on extensive taxon sampling from regions outside of Peninsular India (such as Nepal, Andaman and Nicobar Archipelago of India, and Sri Lanka) will be required to conclusively address the taxonomic status and systematic affinities of some poorly known taxa that were outside of the present work's focal study area.

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Appendix

Table S1 Details of the mitochondrial 16S rRNA genetic samples included in the study. The list is arranged by the order of terminal nodes in the phylogenetic tree shown in Figure 1.

No.	Species	Voucher No.	Accession No.	Locality	Reference
***M. sahyadris* group**					
1	*M. sahyadris*	SDBDU 2005.1152	MZ156076	India: Kerala: Thiruvambady	Present study
2	*M. sahyadris*	SDBDU 2008.408	MZ156077	India: Kerala: Mukkam	Present study
3	*M. sahyadris*	Haplotype: Fsah-In1	AB530604	India: Kerala: Aralam	Hasan *et al.*, 2014
4	*M. sahyadris*	Haplotype: Fsah-In2	AB530605	India: Kerala: Aralam	Hasan *et al.*, 2014
5	*M. sahyadris*	SDBDU 2017.3671	MZ156078	India: Kerala: Madayipara	Present study
6	*M. sahyadris*	SDBDU 2017.3692	MZ156079	India: Kerala: Madayipara	Present study
7	*M. sahyadris*	SDBDU 2005.4680	MZ156080	India: Karnataka: Someshwara	Present study
8	*M. sahyadris*	SDBDU 2015.3068	MZ156081	India: Karnataka: Manipal	Present study
9	*M. sahyadris*	SDBDU 2015.3046	MZ156082	India: Karnataka: Mangalore	Present study
10	*M. sahyadris*	n.a.	AB488893	India: Karnool	Kotaki *et al.*, 2010
11	*M. gomantaki*	SDBDU 2014.2474	MZ156083	India: Maharashtra: Kudal	Present study
12	*M. gomantaki*	SDBDU 2014.2488	MZ156084	India: Maharashtra: Amboli	Present study
13	*M. gomantaki*	SDBDU 2014.2467	MZ156085	India: Maharashtra: Kaasartaka	Present study
14	*M. gomantaki*	SDBDU 2005.2529	MZ156086	India: Maharashtra: Patgaon	Present study
15	*M. gomantaki*	SDBDU 2011.1424	MZ156087	India: Maharashtra: Phansad	Present study
16	*M. gomantaki*	SDBDU 2011.1423	MZ156088	India: Maharashtra: Phansad	Present study
17	*M. gomantaki*	SDBDU 2003.1689	MZ156089	India: Maharashtra: Kadal	Present study
18	*M. gomantaki*	SDBDU 2014.2489	MZ156090	India: Maharashtra: Kudal	Present study
19	*M. gomantaki*	SDBDU 2016.3762	MZ156191	India: Goa: Netravali	Present study
20	*M. gomantaki*	CESF 2289	KR781084	India: Goa	Dinesh *et al.*, 2015
21	*M. gomantaki*	ZSI/WGRC/V/A/867	KR781085	India: Goa: Codal	Dinesh *et al.*, 2015
22	*M. gomantaki*	CESF 2295	KR781086	India: Goa	Dinesh *et al.*, 2015
23	*M. gomantaki*	SDBDU 2016.3379	MZ156092	India: Goa: Codli	Present study
24	*M. gomantaki*	CESF 2306	KR781087	India: Goa	Dinesh *et al.*, 2015
25	*M. krishnan*	SDBDU 2003.40156	MZ156093	India: Karnataka: Jog falls	Present study
26	*M. krishnan*	n.a.	MG870108	India: Karnataka: Jog falls	Raj *et al.*, 2018
***M. agricola* group**					
27	*M. agricola*	SDBDU 2012.1980	MZ156094	India: Karnataka: Bangalore	Present study
28	*M. agricola*	SDBDU 2014.2572	MZ156095	India: Karnataka: Gubbi	Present study
29	*M. agricola*	WHT2665	AY141843	Sri Lanka	Meegaskumbura *et al.*, 2002
30	*M. agricola*	n.a.	AB488892	Sri Lanka: Bentota	Kotaki *et al.*, 2010
31	*M. agricola*	SDBDU 2012.1805	MZ156096	India: Tamil Nadu: Tranquebar	Present study
32	*M. agricola*	SDBDU 2014.2734	MZ156097	India: Tamil Nadu: Mamallapuram	Present study
33	*M. agricola*	SDBDU 2012.1821	MZ156098	India: Tamil Nadu: Pondicherry	Present study
34	*M. agricola*	SDBDU 2014.2799	MZ156099	India: Tamil Nadu: Coimbatore	Present study
35	*M. agricola*	SDBDU 2014.2802	MZ156100	India: Tamil Nadu: Coimbatore	Present study
36	*M. agricola*	SDBDU 2014.2815	MZ156101	India: Tamil Nadu: Peramalkovilpetty	Present study
37	*M. agricola*	SDBDU 2014.2816	MZ156102	India: Tamil Nadu: Peramalkovilpetty	Present study
38	*M. agricola*	SDBDU 2014.2819	MZ156103	India: Tamil Nadu: Peramalkovilpetty	Present study
39	*M. agricola*	SDBDU 2005.4752	MZ156104	India: Tamil Nadu: Coimbatore	Present study
40	*M. agricola*	SDBDU 2002.4025	MZ156105	India: Tamil Nadu: Saravamanpetti	Present study
41	*M. agricola*	SDBDU 2008.1955	MZ156106	India: Tamil Nadu: Vazhayathuvayal	Present study
42	*M. agricola*	SDBDU 2006.4778	MZ156107	India: Kerala: Karamana	Present study
43	*M. agricola*	SDBDU 2008.1983	MZ156108	India: Kerala: Karamana	Present study
44	*M. agricola*	SDBDU 2012.2068	MZ156109	India: Kerala: Karthikappally	Present study
45	*M. agricola*	SDBDU 2012.1847	MZ156110	India: Kerala: Thekkady	Present study
46	*M. agricola*	SDBDU 2012.1848	MZ156111	India: Kerala: Thekkady	Present study
47	*M. agricola*	SDBDU 2012.1854	MZ156112	India: Kerala: Thekkady	Present study
48	*M. agricola*	SDBDU 2006.4779	MZ156113	India: Kerala: Thekkady	Present study
49	*M. agricola*	SDBDU 2005.4598	MZ156114	India: Kerala: Thekkady	Present study
50	*M. agricola*	SDBDU 2006.2502	MZ156115	India: Kerala: Anchurilli, Periyar TR	Present study

Continued Table S1

No.	Species	Voucher No.	Accession No.	Locality	Reference
51	*M. agricola*	SDBDU 2014.2725	MZ156116	India: Kerala: Mattupetty	Present study
52	*M. agricola*	SDBDU 2014.2689	MZ156117	India: Kerala: Munnar	Present study
53	*M. agricola*	SDBDU 2014.2690	MZ156118	India: Kerala: Munnar	Present study
54	*M. agricola*	SDBDU 2011.522	MZ156119	India: Kerala: Parambikulam TR	Present study
55	*M. agricola*	SDBDU 2011.527	MZ156120	India: Kerala: Parambikulam TR	Present study
56	*M. agricola*	SDBDU 2003.40280	MZ156121	India: Kerala: Nelliyampathi	Present study
57	*M. agricola*	SDBDU 2014.2621	MZ156122	India: Kerala: Vythiri	Present study
58	*M. agricola*	SDBDU 2015.2871	MZ156123	India: Kerala: Pozhuthana	Present study
59	*M. agricola*	SDBDU 2012.1948	MZ156124	India: Karnataka: Mysore	Present study
60	*M. agricola*	SDBDU 2012.1977	MZ156125	India: Karnataka: Mahadevnagar	Present study
61	*M. agricola*	SDBDU 2012.245	MZ156126	India: Karnataka: Wattakoli	Present study
62	*M. agricola*	SDBDU 2012.2193	MZ156127	India: Karnataka: Sakleshpur	Present study
63	*M. agricola*	SDBDU 2014.2526	MZ156128	India: Karnataka: Bannerghatta	Present study
64	*M. agricola*	SDBDU 2014.2562	MZ156129	India: Karnataka: Bannerghatta	Present study
65	*M. agricola*	SDBDU 2014.2563	MZ156130	India: Karnataka: Bannerghatta	Present study
66	*M. agricola*	SDBDU 2014.2570	MZ156131	India: Karnataka: Gubbi	Present study
67	*M. agricola*	SDBDU 2014.2571	MZ156132	India: Karnataka: Gubbi	Present study
68	*M. agricola*	SDBDU 2011.41	MZ156133	India: Karnataka: Kachigebailu, Shimoga	Present study
69	*M. agricola*	SDBDU 2003.40140	MZ156134	India: Karnataka: Hurugodlu, Shimoga	Present study
70	*M. agricola*	SDBDU 2017.3681	MZ156135	India: Karnataka: Mavingundi	Present study
71	*M. agricola*	SDBDU 2011.1317	MZ156136	India: Karnataka: Dandeli	Present study
72	*M. agricola*	BNHS 4651	AB488895	India: Karnataka: Mudigere	Kotaki *et al.*, 2010
73	*M. agricola*	BNHS 4649	AB355836	India: Karnataka: Madikeri	Kuramoto *et al.*, 2008 "2007"
74	*M. agricola*	BNHS 4650	AB355837	India: Karnataka: Talagini	Kuramoto *et al.*, 2008 "2007"
75	*M. agricola*	BNHS 4652	AB355839	India: Karnataka: Madikeri	Kuramoto *et al.*, 2008 "2007"
76	*M. agricola*	n.a.	AF249040	India	Bossuyt and Milinkovitch, 2000
77	*M. agricola*	haplotype:hpA-2	AB167948	India: Karnataka: Madikeri	Kurabayashi *et al.*, 2005
78	*M. agricola*	n.a.	MH370482	India: Maharashtra: Pune	Phuge *et al.*, 2020
79	*M. agricola*	D214	MK713347	India: Maharashtra: Koyna	Phuge *et al.*, 2020
80	*M. agricola*	n.a.	KR995134	India	Jesmina and George (unpublished)
81	*M. agricola*	SDBDU 2012.1868	MZ156137	India: Kerala: Thiruvalla	Present study
82	*M. agricola*	SDBDU 2012.1954	MZ156138	India: Karnataka: Vijaynagar	Present study
83	*M. agricola*	n.a.	GQ478321	India	Meenakshi *et al.*, 2010
84	*M. agricola*	SDBDU 2014.2541	KY820766	India: Karnataka: BR Hills	Garg and Biju, 2017
85	*M. agricola*	BNHS 4651	AB355838	India: Karnataka: Mudigere	Kuramoto *et al.*, 2008 "2007"
86	*M. agricola*	0318_455_005	MK628927	India: Pondicherry	Chandramouli *et al.*, 2019
87	*M. agricola*	BFS-127	AB372016	Bangladesh: Cox's Bazar	Islam *et al.*, 2008
88	*M. agricola*	BFS-129	AB372017	Bangladesh: Cox's Bazar	Islam *et al.*, 2008
89	*M. agricola*	haplotype:Fsp.S-Bd2	AB530510	Bangladesh: Cox's Bazar: Laboni point	Hasan *et al.*, 2012
90	*M. agricola*	IN008	AY841756	India	Guha *et al.* (unpublished)
91	*M. agricola*	IN0011	AY841751	India	Guha *et al.* (unpublished)
92	*M. agricola*	IN0010	AY841750	India	Guha *et al.* (unpublished)
93	*M. agricola*	IN006	AY841747	India	Guha *et al.* (unpublished)
94	*M. agricola*	IN021	AY882953	India	Tandon *et al.* (unpublished)
95	*M. agricola*	SDBDU 2013.2429	MZ156139	India: Rajasthan: Bharatpur	Present study
96	*M. agricola*	SDBDU 2012.2284	MZ156140	India: Punjab: Amritsar	Present study
97	*M. agricola*	SDBDU 2012.1935	MZ156141	India: Haryana: Morni Hills	Present study
98	*M. agricola*	SDBDU 2006.4870	MZ156142	India: Delhi	Present study
99	*M. agricola*	SDBDU 2012.1913	MZ156143	India: Uttar Pradesh: Bijnore	Present study
100	*M. agricola*	SDBDU 2018.3752	MZ156144	India: Uttarakhand: Dehradun	Present study
101	*M. agricola*	SDBDU 2012.1923	MZ156145	India: Uttarakhand: Guchupani	Present study
102	*M. agricola*	SDBDU 2010.168	MZ156146	India: Uttarakhand: Sahiya	Present study
103	*M. agricola*	SDBDU 2010.118	MZ156147	India: Uttarakhand: Utrala	Present study
104	*M. agricola*	IABHU 34056/ 34057	AB488888	Nepal: Chitwan	Kotaki *et al.*, 2010
105	*M. agricola*	SDBDU 2011.875	MZ156148	India: Bihar: Kaitha	Present study
106	*M. agricola*	SDBDU 2015.2923	MZ156149	India: West Bengal: Howrah	Present study

Continued Table S1

No.	Species	Voucher No.	Accession No.	Locality	Reference
107	*M. agricola*	SDBDU 2015.2917	MZ156150	India: Assam: Guwahati	Present study
108	*M. agricola*	BFS-50	AB372012	Bangladesh: Mymensingh: BAU Campus	Islam *et al.*, 2008
109	*M. agricola*	haplotype: Fsp.S-Bd1	AB530509	Bangladesh: Mymensingh: Char Nilokhia	Hasan *et al.*, 2012
110	*M. agricola*	F1DSE_14	KP849816	Bangladesh	Howlader *et al.*, 2016
111	*M. agricola*	FSP 02	MK635481	Bangladesh	Jahan *et al.* (unpublished)
112	*M. agricola*	BFS-66	AB372014	Bangladesh: Dinajpur: Parbatipur	Islam *et al.*, 2008
113	*M. agricola*	BFS-91	AB372015	Bangladesh: Kishoreganj: Tarail	Islam *et al.*, 2008
114	*M. agricola*	FSP 04	MK635483	Bangladesh	Jahan *et al.* (unpublished)
115	*M. agricola*	SDBDU 2012.2164	MZ156151	India: Rajasthan: Jaipur	Present study
116	*M. agricola*	IN007	AY841748	India	Guha *et al.* (unpublished)
117	*M. agricola*	SDBDU 2007.5083	MZ156152	India: Andhra Pradesh: Araku Valley	Present study
118	*M. agricola*	SDBDU 2007.5055	MZ156153	India: Andhra Pradesh: Vishakapatnam	Present study
119	*M. agricola*	SDBDU 2005.1754	MZ156154	India: Maharashtra: Yawal WLS	Present study
120	*M. agricola*	SDBDU 2018.3781	MZ156155	India: Maharashtra: Yedshi-Ramling	Present study
121	*M. agricola*	SDBDU 2008.4373	MZ156156	India: Gujarat: Valsad	Present study
122	*M. agricola*	SDBDU 2008.4402	MZ156157	India: Gujarat: Surat	Present study
123	*M. agricola*	SDBDU 2008.4404	MZ156158	India: Gujarat: Dang	Present study
124	*M. agricola*	SDBDU 2011.588	MZ156159	India: Chhattisgarh: Dharampani	Present study
125	*M. agricola*	SDBDU 2015.3124	MZ156160	India: Odisha: Dhuanhalli	Present study
126	*M. agricola*	IN023	AY882955	India	Tandon *et al.* (unpublished)
127	*M. agricola*	IN022	AY882954	India	Tandon *et al.* (unpublished)
128	*M. agricola*	SDBDU 2005.1756	MZ156161	India: Maharashtra: Yawal WLS	Present study
129	*M. agricola*	IN018	AY882950	India	Tandon *et al.* (unpublished)
130	*M. agricola*	IN017	AY882949	India	Tandon *et al.* (unpublished)
131	*M. agricola*	IN020	AY882952	India	Tandon *et al.* (unpublished)
132	*M. agricola*	BFS-71	AB372013	Bangladesh: Mymensingh: BAU Campus	Islam *et al.*, 2008
133	*M. asmati*	n.a.	AB488900	India: Assam	Kotaki *et al.*, 2010
134	*M. asmati*	SL115	MF319217	India: Mizoram "23.708 N 92.641 E"	Lalronunga *et al.* (unpublished)
135	*M. asmati*	FSP 03	MK635482	Bangladesh	Jahan *et al.* (unpublished)
136	*M. asmati*	FaCSE_17	KP849815	Bangladesh	Howlader *et al.*, 2016
137	*M. asmati*	A16	MF319215	India: Mizoram "23.713 N 92.667 E"	Lalronunga *et al.* (unpublished)
138	*M. asmati*	SL121	MF319219	India: Mizoram "23.703 N 92.714 E"	Lalronunga *et al.* (unpublished)
139	*M. teraiensis*	isolate: BFM-40	AB372011	Bangladesh: Mymensingh: BAU Campus	Islam *et al.*, 2008
140	*M. teraiensis*	haplotype: Fsp.M-Bd	AB530511	Bangladesh: Mymensingh: BAU Campus	Hasan *et al.*, 2012
141	*M. teraiensis*	F1DSE_15	KP849817	Bangladesh	Howlader *et al.*, 2016
142	*M. teraiensis*	F1DSE_2	KP849818	Bangladesh	Howlader *et al.*, 2016
143	*M. teraiensis*	F1DSE_23	KP849819	Bangladesh	Howlader *et al.*, 2016
144	*M. teraiensis*	FSP 01	MK635480	Bangladesh	Jahan *et al.* (unpublished)
145	*M. teraiensis*	FSP 05	MK635484	Bangladesh	Jahan *et al.* (unpublished)
146	*M. teraiensis*	FSP 07	MK635486	Bangladesh	Jahan *et al.* (unpublished)
147	*M. teraiensis*	HJZG-04	MG010390	Bangladesh	Jahan *et al.* (unpublished)
148	*M. chiangmaiensis*	KIZ 024057	KX834135	Thailand: Chiang Mai; Omkoi	Suwannapoom *et al.*, 2016
149	*M. chiangmaiensis*	KIZ 024126	KX834136	Thailand: Chiang Mai; Omkoi	Suwannapoom *et al.*, 2016
***M. syhadrensis* group**					
150	*M. syhadrensis*	IN024	AY882956	India	Tandon *et al.* (unpublished)
151	*M. syhadrensis*	BNHS 4659	AB355844	India: Karnataka: Talagini	Kuramoto *et al.*, 2008 "2007"
152	*M. syhadrensis*	SDBDU 2012.2090	MZ156162	India: Goa: Calangute	Present study
153	*M. syhadrensis*	IN019	AY882951	India	Tandon *et al.* (unpublished)
154	*M. syhadrensis*	BNHS 4660	AB355845	India: Karnataka: Madikeri	Kuramoto *et al.*, 2008 "2007"
155	*M. syhadrensis*	SDBDU 2007.5075	MZ156163	India: Andhra Pradesh: Borra Caves	Present study
156	*M. syhadrensis*	IN013	AY841752	India	Guha *et al.* (unpublished)
157	*M. syhadrensis*	n.a.	MH370481	India: Maharashtra: Pune	Phuge *et al.*, 2020
158	*M. syhadrensis*	SDBDU 2018.3729	MZ156164	India: Odisha: Similipal TR	Present study
159	*M. syhadrensis*	D215	MK713346	India: Karnataka: Aldur	Phuge *et al.*, 2020
160	*M. syhadrensis*	D211	MK713344	India: Goa	Phuge *et al.*, 2020
161	*M. syhadrensis*	030526-02	AB167954	India: Karnataka: Mangalore, Bajipe	Kurabayashi *et al.*, 2005

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No.	Species	Voucher No.	Accession No.	Locality	Reference
162	*M. syhadrensis*	BNHS 4658	AB355843	India: Karnataka: Mangalore	Kuramoto *et al.*, 2008 "2007"
163	*M. syhadrensis*	BNHS 4657	AB355842	India: Karnataka: Karnoor	Kuramoto *et al.*, 2008 "2007"
164	*M. syhadrensis*	isolate 3066/ BNHS 5060	AB488894	India: Karnataka: Mudigere	Kotaki *et al.*, 2010
165	*M. syhadrensis*	SDBDU 2008.4393	MZ156165	India: Gujarat: Dang, Purna WLS	Present study
166	*M. syhadrensis*	SDBDU 2008.4384	MZ156166	India: Gujarat: Navsari, Vansda NP	Present study
167	*M. syhadrensis*	SDBDU 2008.4377	MZ156167	India: Gujarat: Ruzuvani	Present study
168	*M. syhadrensis*	SDBDU 2010.393	MZ156168	India: Chhattisgarh: Amarkantak–Achanakmar	Present study
169	*M. syhadrensis*	SDBDU 2011.584	MZ156169	India: Madhya Pradesh: Amarkantak	Present study
170	*M. syhadrensis*	SDBDU 2018.3736	MZ156170	India: Odisha: Bhubaneswar	Present study
171	*M. syhadrensis*	SDBDU 2018.3728	MZ156171	India: Odisha: Similipal TR	Present study
172	*M. syhadrensis*	SDBDU 2015.3110	MZ156172	India: Odisha: Barbara	Present study
173	*M. syhadrensis*	SDBDU 2007.5031	MZ156173	India: Andhra Pradesh: Maredumilli	Present study
174	*M. syhadrensis*	SDBDU 2007.5051A	MZ156174	India: Andhra Pradesh: Chintapalle	Present study
175	*M. syhadrensis*	SDBDU 2005.1755	MZ156175	India: Maharashtra: Yawal WLS	Present study
176	*M. syhadrensis*	SDBDU 2014.2507	MZ156176	India: Maharashtra: Tungareshwar WLS	Present study
177	*M. syhadrensis*	SDBDU 2012.2092	MZ156177	India: Maharashtra: Vashi	Present study
178	*M. syhadrensis*	SDBDU 2017.3664	MZ156178	India: Maharashtra: Matheran	Present study
179	*M. syhadrensis*	SDBDU 2011.1464	MZ156179	India: Maharashtra: Matheran	Present study
180	*M. syhadrensis*	SDBDU 2011.1463	MZ156180	India: Maharashtra: Neral	Present study
181	*M. syhadrensis*	SDBDU 2011.1430	MZ156181	India: Maharashtra: Phansad	Present study
182	*M. syhadrensis*	SDBDU 2015.2934	MZ156182	India: Maharashtra: Pune	Present study
183	*M. syhadrensis*	SDBDU 2014.2680	MZ156183	India: Maharashtra: Pune	Present study
184	*M. syhadrensis*	SDBDU 2012.2103	MZ156184	India: Maharashtra: Lavasa	Present study
185	*M. syhadrensis*	SDBDU 2012.2146	MZ156185	India: Maharashtra: Koyna	Present study
186	*M. syhadrensis*	SDBDU 2001.1411	MZ156186	India: Maharashtra: Koyna	Present study
187	*M. syhadrensis*	SDBDU 2005.2525	MZ156187	India: Maharashtra: Wagh Zara	Present study
188	*M. syhadrensis*	SDBDU 2005.2523	MZ156188	India: Maharashtra: Wagh Zara	Present study
189	*M. syhadrensis*	SDBDU 2014.2472	MZ156189	India: Maharashtra: Amboli	Present study
190	*M. syhadrensis*	SDBDU 2012.2132	MZ156190	India: Maharashtra: Amboli	Present study
191	*M. syhadrensis*	SDBDU 2016.3398	MZ156191	India: South Goa: Netravali	Present study
192	*M. syhadrensis*	SDBDU 2016.3396	MZ156192	India: South Goa: Netravali	Present study
193	*M. syhadrensis*	SDBDU 2011.839	MZ156193	India: Karnataka: Castle rock	Present study
194	*M. syhadrensis*	SDBDU 2011.516	MZ156194	India: Karnataka: Bygoor	Present study
195	*M. syhadrensis*	SDBDU 2012.2217	MZ156195	India: Karnataka: Gallebedu	Present study
196	*M. syhadrensis*	SDBDU 2005.4688	MZ156196	India: Karnataka: Someshwar	Present study
197	*M. syhadrensis*	SDBDU 2001.1442	MZ156197	India: Karnataka: Madikeri	Present study
198	*M. syhadrensis*	SDBDU 2012.252	MZ156198	India: Karnataka: Wattakoli	Present study
199	*M. syhadrensis*	SDBDU 2014.2516	MZ156199	India: Karnataka: Agumbe	Present study
200	*M. syhadrensis*	SDBDU 2017.3677	MZ156200	India: Karnataka: Mavingundi	Present study
201	*M. syhadrensis*	SDBDU 2017.3605	MZ156201	India: Kerala: Anakallu	Present study
202	*M. syhadrensis*	SDBDU 2011.1419	MZ156202	India: Karnataka: Adyar	Present study
203	*M. syhadrensis*	SDBDU 2011.1414	MZ156203	India: Karnataka: Bajipe	Present study
204	*M. syhadrensis*	SDBDU 2015.3058	MZ156204	India: Karnataka: Manipal	Present study
205	*M. syhadrensis*	SDBDU 2015.3049	MZ156205	India: Karnataka: Mangalore	Present study
206	*M. syhadrensis*	SDBDU 2015.2872	MZ156206	India: Kerala: Pozhuthana	Present study
207	*M. syhadrensis*	SDBDU 2015.3136	MZ156207	India: Kerala: Vazhachal	Present study
208	*M. syhadrensis*	SDBDU 2015.3037	MZ156208	India: Kerala: Parambikulam TR	Present study
209	*M. syhadrensis*	SDBDU 2012.921	MZ156209	India: Kerala: Vagamon	Present study
210	*M. syhadrensis*	SDBDU 2001.1330	MZ156210	India: Kerala: Kalpetta	Present study
211	*M. syhadrensis*	SDBDU 2014.2619	MZ156211	India: Kerala: Vythiri	Present study
212	*M. syhadrensis*	SDBDU 2014.2601	MZ156212	India: Kerala: Calicut	Present study
213	*M. syhadrensis*	SDBDU 2012.2042	MZ156213	India: Kerala: Kadakkattupara	Present study
214	*M. syhadrensis*	SDBDU 2012.2036	MZ156214	India: Kerala: Thenjipalam	Present study
215	*M. syhadrensis*	IN014	AY841753	India	Guha *et al.* (unpublished)
216	*M. syhadrensis*	IN012	AY841755	India	Guha *et al.* (unpublished)
217	*M. syhadrensis*	SDBDU 2012.2213	MZ156215	India: Karnataka: Sakleshpur	Present study

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No.	Species	Voucher No.	Accession No.	Locality	Reference
218	*M. syhadrensis*	SDBDU 2012.2184	MZ156216	India: Karnataka: Mudigere	Present study
219	*M. syhadrensis*	D210	MK713343	India: Maharashtra: Koyna	Phuge *et al.*, 2020
220	*M. nepalensis*	n.a.	AB488889	Nepal: Chitwan	Kotaki *et al.*, 2010
221	*M. pentali* **sp. nov.**	SDBDU 2012.2070	MZ156217	India: Kerala: Karthikappally	Present study
222	*M. pentali* **sp. nov.**	SDBDU 2008.1956	MZ156218	India: Tamil Nadu: Vazhayathuvayal	Present study
223	*M. pentali* **sp. nov.**	SDBDU 2003.40124	MZ156219	India: Kerala: Chathankod	Present study
224	*M. pentali* **sp. nov.**	SDBDU 2014.2645	MZ156220	India: Kerala: Chathankod	Present study
225	*M. pentali* **sp. nov.**	SDBDU 2015.2967	MZ156221	India: Kerala: Karamana	Present study
226	*M. pentali* **sp. nov.**	SDBDU 2012.1871	MZ156222	India: Kerala: Kulanada	Present study
227	*M. pentali* **sp. nov.**	SDBDU 2003.40228	MZ156223	India: Kerala: Thrissur	Present study
228	*M. pentali* **sp. nov.**	SDBDU 2008.1967	MZ156224	India: Kerala: Kuriyode	Present study
229	*M. pentali* **sp. nov.**	SDBDU 2006.4787	MZ156225	India: Kerala: Nilamel	Present study
230	*M. pentali* **sp. nov.**	SDBDU 2017.3628	MZ156226	India: Kerala: Kuriyode	Present study
231	*M. pentali* **sp. nov.**	SDBDU 2015.3129	MZ156227	India: Kerala: Calicut	Present study
232	*M. pentali* **sp. nov.**	SDBDU 2012.2043	MZ156228	India: Kerala: Kadakkattupara	Present study
233	*M. pentali* **sp. nov.**	BNHS 6116	MZ156229	India: Kerala: Nedumbaserry	Present study
***M. brevipalmata* group**					
234	*M. brevipalmata*	SDBDU 2011.1048	MZ156230	India: Kerala: Kadalar	Present study
235	*M. brevipalmata*	SDBDU 2012.818	MZ156231	India: Kerala: Kadalar	Present study
236	*M. brevipalmata*	SDBDU 2012.872	MZ156232	India: Kerala: Kadalar	Present study
237	*M. brevipalmata*	SDBDU 2014.2701	MZ156233	India: Kerala: Devikulam	Present study
238	*M. brevipalmata*	SDBDU 2014.2698	MZ156234	India: Kerala: Kadalar	Present study
239	*M. brevipalmata*	SDBDU 2014.2715	MZ156235	India: Kerala: Mattupetty	Present study
240	*M. brevipalmata*	SDBDU 2014.2724	MZ156236	India: Kerala: Munnar	Present study
241	*M. brevipalmata*	SDBDU 2002.1644	MZ156237	India: Kerala: Munnar	Present study
242	*M. brevipalmata*	SDBDU 2001.1333	MZ156238	India: Kerala: Eravikulam NP	Present study
243	*M. brevipalmata*	SDBDU 2006.4786	MZ156239	India: Kerala: Anchuruli	Present study
244	*M. brevipalmata*	SDBDU 2008.1978	MZ156240	India: Kerala: Periyar TR	Present study
245	*M. brevipalmata*	SDBDU 2012.1834	MZ156241	India: Kerala: Thekkady	Present study
246	*M. brevipalmata*	SDBDU 2015.2986	MZ156242	India: Kerala: Kozhikana	Present study
247	*M. brevipalmata*	SDBDU 2016.3354	MZ156243	India: Kerala: Eravangalar	Present study
248	*M. brevipalmata*	SDBDU 2015.2997	MZ156244	India: Tamil Nadu: Meghamalai	Present study
249	*M. goemchi*	SDBDU 2001.1554	MZ156245	India: Maharashtra: Koyna	Present study
250	*M. goemchi*	SDBDU 2001.1412	MZ156246	India: Maharashtra: Koyna	Present study
251	*M. goemchi*	SDBDU 2010.344	MZ156247	India: Maharashtra: Koyna	Present study
252	*M. goemchi*	SDBDU 2010.343	MZ156248	India: Maharashtra: Koyna	Present study
253	*M. goemchi*	SDBDU 2013.2356	MZ156249	India: Maharashtra: Mahabaleshwar	Present study
254	*M. goemchi*	SDBDU 2011.837	MZ156250	India: Karnataka: Castle rock	Present study
255	*M. goemchi*	SDBDU 2013.2439	MZ156251	India: Maharashtra: Amboli	Present study
256	*M. goemchi*	SDBDU 2014.2484	MZ156252	India: Maharashtra: Amboli	Present study
257	*M. goemchi*	SDBDU 2014.2485	MZ156253	India: Maharashtra: Amboli	Present study
258	*M. goemchi*	SDBDU 2015.3095A	MZ156254	India: Maharashtra: Amboli	Present study
259	*M. goemchi*	SDBDU 2015.3095B	MZ156255	India: Maharashtra: Amboli	Present study
260	*M. goemchi*	SDBDU 2014.2480	MZ156256	India: Maharashtra: Amboli	Present study
261	*M. goemchi*	SDBDU 2014.2481	MZ156257	India: Maharashtra: Amboli	Present study
262	*M. goemchi*	SDBDU 2005.4225	MZ156258	India: Maharashtra: Amboli	Present study
263	*M. goemchi*	SDBDU 2001.1432	MZ156259	India: Maharashtra: Amboli	Present study
264	*M. goemchi*	SDBDU 2001.1435	MZ156260	India: Maharashtra: Amboli	Present study
265	*M. goemchi*	SDBDU 2002.1655	MZ156261	India: Maharashtra: Amboli	Present study
266	*M. goemchi*	SDBDU 2003.40202	MZ156262	India: Karnataka: Castle rock	Present study
267	*M. goemchi*	ZSI/WRC/A/2017	MG800343	India: Goa: Surla	Dinesh *et al.*, 2017
268	*M. goemchi*	CESF 2843	MG800344	India: Goa: Surla	Dinesh *et al.*, 2017
269	*M. mysorensis*	SDBDU 2012.85	MZ156263	India: Karnataka: Coorg	Present study
270	*M. mysorensis*	SDBDU 2012.98	MZ156264	India: Karnataka: Bhagamandala	Present study
271	*M. mysorensis*	SDBDU 2012.213	MZ156265	India: Karnataka: Thalakaveri	Present study
272	*M. mysorensis*	SDBDU 2012.238	MZ156266	India: Karnataka: Wattakoli	Present study

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No.	Species	Voucher No.	Accession No.	Locality	Reference
273	*M. mysorensis*	BNHS 6114	MZ156267	India: Karnataka: Wattakoli	Present study
274	*M. mysorensis*	SDBDU 2012.250	MZ156268	India: Karnataka: Wattakoli	Present study
275	*M. mysorensis*	BNHS 4655	AB355840	India: Karnataka: Madikeri	Kuramoto *et al.*, 2008 "2007"
276	*M. mysorensis*	SDBDU 2014.2617	MZ156269	India: Kerala: Vythiri–Pozuthana	Present study
277	*M. mysorensis*	SDBDU 2017.3521	MZ156270	India: Kerala: Vythiri	Present study
278	*M. mysorensis*	SDBDU 2015.2878	MZ156271	India: Kerala: Kalloor	Present study
279	*M. mysorensis*	SDBDU 2002.1743	MZ156272	India: Kerala: Wayanad	Present study
280	*M. mysorensis*	SDBDU 2015.2855	MZ156273	India: Kerala: Suganthagiri	Present study
281	*M. mysorensis*	SDBDU 2014.2598	MZ156274	India: Kerala: Vythiri	Present study
282	*M. mysorensis*	SDBDU 2014.2613	MZ156275	India: Kerala: Suganthagiri	Present study
283	*M. mysorensis*	SDBDU 2005.4734	MZ156276	India: Kerala: Pozhuthana	Present study
284	*M. mysorensis*	SDBDU 2014.2506	MZ156277	India: Karnataka: Agumbe	Present study
285	*M. mysorensis*	SDBDU 2001.1332	MZ156278	India: Karnataka: Jog	Present study
286	*M. mysorensis*	SDBDU 2003.40214	MZ156279	India: Karnataka: Kemanagudi	Present study
287	*M. mysorensis*	SDBDU 2011.514	MZ156280	India: Karnataka: Bygoor	Present study
288	*M. mysorensis*	SDBDU 2002.1067	MZ156281	India: Karnataka: Sakleshpur	Present study
289	*M. mysorensis*	030610-07	AB167949	India: Karnataka: Kudremukh	Kurabayashi *et al.*, 2005
290	*M. mysorensis*	030610-08	AB167950	India: Karnataka: Kudremukh	Kurabayashi *et al.*, 2005
291	*M. mysorensis*	BNHS 4653/ 4654	AB488898	India: Karnataka: Kudremukh	Kotaki *et al.*, 2010
292	*M. mysorensis*	BNHS 4656	AB355841	India: Karnataka: Mudigere	Kuramoto *et al.*, 2008 "2007"
293	*M. mysorensis*	SDBDU 2002.1648	MZ156282	India: Kerala: Kaikatti	Present study
294	*M. mysorensis*	SDBDU 2015.3036B	MZ156283	India: Kerala: Parambikulam TR	Present study
295	*M. mysorensis*	BNHS 6113	MZ156284	India: Kerala: Theenakadav, Parambikulam TR	Present study
296	*M. mysorensis*	SDBDU 2001.781	MZ156285	India: Tamil Nadu: Puthuthottam	Present study
***M. greenii* group**					
297	*M. greenii*	MNHN 2000.617	AB488891	Sri Lanka: Nuwara Eliya	Kotaki *et al.*, 2010
298	*M. kirtisinghei*	MNHN 2000.620	AY014380	Sri Lanka: Laggalla	Kosuch *et al.*, 2001
299	*M. kirtisinghei*	MNHN 2000.620	AB488890	Sri Lanka: Laggalla	Kotaki *et al.*, 2010
***M. rufescens* group**					
300	*M. rufescens*	SDBDU 2015.3070	KY447321	India: Karnataka: Manipal	Garg and Biju, 2017
301	*M. rufescens*	SDBDU 2009.4712	KY447320	India: Karnataka: Kollur, Mookambika	Garg and Biju, 2017
302	*M. rufescens*	SDBDU 2013.2505	KY447319	India: Karnataka: Guddekere, Agumbe	Garg and Biju, 2017
303	*M. rufescens*	SDBDU 2008.407	KY447322	India: Kerala: Peruvannamuzhi	Garg and Biju, 2017
304	*M. rufescens*	SDBDU 2015.2882	KY447323	India: Kerala: Pozhuthana	Garg and Biju, 2017
305	*M. rufescens*	SDBDU 2017.3575	MZ156286	India: Kerala: Ranipuram	Present study
306	*M. rufescens*	n.a.	AB488897	India: Karnataka: Madikeri	Kotaki *et al.*, 2010
307	*M. rufescens*	030526-03	AB167945	India: Karnataka: Mangalore, Bajipe	Kurabayashi *et al.*, 2005
308	*M. rufescens*	Haplotype: Fruf-In1	AB530601	India: Karnataka: Mangalore, Bajipe	Hasan *et al.*, 2014
309	*M. kadar*	ZSI/WGRC/V/A/940	KY447312	India: Kerala: Thavalakuzhipara	Garg and Biju, 2017
310	*M. manoharani*	SDBDU 2011.275	KY447316	India: Kerala: Kattalapara	Garg and Biju, 2017
311	*M. manoharani*	ZSI/WGRC/V/A/950	KY447315	India: Kerala: Chathankod-Bonnacad	Garg and Biju, 2017
312	*M. manoharani*	ZSI/WGRC/V/A/945	KY447313	India: Kerala: Chathankod-Bonnacad	Garg and Biju, 2017
313	*M. manoharani*	SDBDU 2013.2669	KY447314	India: Kerala: Chathankod-Bonnacad	Garg and Biju, 2017
314	*M. neilcoxi*	ZSI/WGRC/V/A/955	KY447317	India: Kerala: Parambikulam	Garg and Biju, 2017
315	*M. neilcoxi*	ZSI/WGRC/V/A/951	KY447318	India: Kerala: Parambikulam	Garg and Biju, 2017
316	*M. cepfi*	SDBDU 2012.1429	KY447311	India: Maharashtra: Phansad WLS	Garg and Biju, 2017
317	*M. cepfi*	SDBDU 2007.1569	KY447310	India: Maharashtra: Koyna	Garg and Biju, 2017
318	*M. cepfi*	SDBDU 2007.1561	KY447309	India: Maharashtra: Koyna	Garg and Biju, 2017
319	*M. cepfi*	ZSI/WGRC/V/A/938	KY447308	India: Maharashtra: Amboli	Garg and Biju, 2017
***M. andamanensis* group**					
320	*M. marathi*	SDBDU 2011.1103	MZ156287	India: Maharashtra: Bhimashankar	Present study
321	*M. marathi*	SDBDU 2011.1104	MZ156288	India: Maharashtra: Bhimashankar	Present study
322	*M. marathi*	SDBDU 2013.2368	MZ156289	India: Maharashtra: Tungareshwar NP	Present study
323	*M. marathi*	SDBDU 2014.2510	MZ156290	India: Maharashtra: Sanjay Gandhi NP	Present study
324	*M. marathi*	SDBDU 2015.2940	MZ156291	India: Maharashtra: Tahmini ghat	Present study
325	*M. marathi*	n.a.	MH370483	India: Maharashtra: Pune, Bhamburde	Phuge *et al.*, 2019

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No.	Species	Voucher No.	Accession No.	Locality	Reference
326	*M. andamanensis*	n.a.	AB488899	India: Andaman Island	Kotaki *et al.*, 2010
327	*M. muangkanensis*	KIZ 024627	MF166918	Thailand: Kanchanaburi; Thong Pha Phum	Suwannapoom *et al.*, 2017
328	*M. muangkanensis*	IABHU 18145 /18156 /18157	AB277300	Thailand: Pilok	Kotaki *et al.*, 2008
***M. nilagirica* group**					
329	*M. keralensis*	SDBDU 2011.257	MZ156292	India: Kerala: Ponmudi	Present study
330	*M. keralensis*	SDBDU 2011.267	MZ156293	India: Kerala: Chathankod–Makki	Present study
331	*M. keralensis*	SDBDU 2001.791	MZ156294	India: Kerala: Bonnacad	Present study
332	*M. keralensis*	SDBDU 2015.2928	MZ156295	India: Kerala: Kuttayar, Peepara WLS	Present study
333	*M. keralensis*	SDBDU 2011.273	MZ156296	India: Kerala: Shendurney WLS	Present study
334	*M. keralensis*	SDBDU 2002.4045	MZ156297	India: Kerala: Shencottah	Present study
335	*M. keralensis*	SDBDU 2015.3139	MZ156298	India: Kerala: Vazhachal	Present study
336	*M. keralensis*	SDBDU 2015.3141	MZ156299	India: Kerala: Thavalakuzhipara	Present study
337	*M. keralensis*	SDBDU 2015.3163	MZ156300	India: Kerala: Malakkapara	Present study
338	*M. keralensis*	SDBDU 2011.2736	MZ156301	India: Kerala: Kulamav	Present study
339	*M. keralensis*	SDBDU 2012.2006	MZ156302	India: Kerala: Methooty	Present study
340	*M. keralensis*	SDBDU 2012.2022	MZ156303	India: Kerala: Poomala	Present study
341	*M. keralensis*	SDBDU 2012.1832	MZ156304	India: Kerala: Thekkady	Present study
342	*M. keralensis*	SDBDU 2011.528	MZ156305	India: Kerala: Parambikulam TR	Present study
343	*M. keralensis*	SDBDU 2011.529	MZ156306	India: Kerala: Parambikulam TR	Present study
344	*M. keralensis*	SDBDU 2011.530	MZ156307	India: Kerala: Parambikulam TR	Present study
345	*M. keralensis*	SDBDU 2011.1216	MZ156308	India: Kerala: Kesavapara	Present study
346	*M. keralensis*	SDBDU 2010.265	MZ156309	India: Kerala: Nelliyampathy	Present study
347	*M. keralensis*	SDBDU 2002.876	MZ156310	India: Tamil Nadu: Sengaltheri	Present study
348	*M. keralensis*	SDBDU 2008.1942	MZ156311	India: Tamil Nadu: Glenbeck estate	Present study
349	*M. keralensis*	SDBDU 2008.2098	MZ156312	India: Tamil Nadu: Kalakkad	Present study
350	*M. keralensis*	n.a.	GQ478322	India	Meenakshi *et al.*, 2010
351	*M. keralensis*	SDBDU 2008.1951	MZ156313	India: Tamil Nadu: Maramalai-Kiripara	Present study
352	*M. keralensis*	WII: 3263	JX573181	India	Raj *et al.*, 2018
353	*M. kalinga*	SDBDU 2015.3395	MZ156314	India: Goa: Netravali	Present study
354	*M. kalinga*	SDBDU 2007.5041	MZ156315	India: Andhra Pradesh: Maredumilli	Present study
355	*M. kalinga*	SDBDU 2015.3108	MZ156316	India: Odisha: Barbara Reserve Forest	Present study
356	*M. kalinga*	SDBDU 2007.5051B	MZ156317	India: Andhra Pradesh: Chintapalle	Present study
357	*M. kalinga*	n.a.	MG870107	India: Odisha	Raj *et al.*, 2018
358	*M. kalinga*	SDBDU 2012.2115	MZ156318	India: Maharashtra: Amboli	Present study
359	*M. nilagirica*	SDBDU 2011.488	MZ156319	India: Tamil Nadu: Naduvattam	Present study
360	*M. nilagirica*	SDBDU 2011.489	MZ156320	India: Tamil Nadu: Naduvattam	Present study
361	*M. nilagirica*	SDBDU 2011.497	MZ156321	India: Tamil Nadu: Naduvattam	Present study
362	*M. nilagirica*	SDBDU 2011.498	MZ156322	India: Tamil Nadu: Naduvattam	Present study
363	*M. nilagirica*	SDBDU 2014.2772	MZ156323	India: Tamil Nadu: Thai Shola	Present study
364	*M. nilagirica*	SDBDU 2014.2776	MZ156324	India: Tamil Nadu: Cairn Hills	Present study
365	*M. nilagirica*	SDBDU 2001.1329	MZ156325	India: Tamil Nadu: T.R. Bazar	Present study
366	*M. nilagirica*	SDBDU 2001.1456	MZ156326	India: Tamil Nadu: Mukurthi	Present study
367	*M. nilagirica*	SDBDU 2001.1457	MZ156327	India: Tamil Nadu: Bangithapal	Present study
368	*M. nilagirica*	SDBDU 2002.1643	MZ156328	India: Tamil Nadu: Nadukani	Present study
369	*M. nilagirica*	SDBDU 2002.1653	MZ156329	India: Tamil Nadu: Coonoor	Present study
370	*M. nilagirica*	SDBDU 2014.2757	MZ156330	India: Tamil Nadu: Avalanche	Present study
371	*M. nilagirica*	SDBDU 2014.2758	MZ156331	India: Tamil Nadu: Avalanche	Present study
372	*M. nilagirica*	SDBDU 2014.2768	MZ156332	India: Tamil Nadu: Korkunda estate	Present study
373	*M. nilagirica*	SDBDU 2002.1683	MZ156333	India: Tamil Nadu: Kollimala	Present study
374	*M. nilagirica*	SDBDU 2011.1253	MZ156334	India: Kerala: Pattiar	Present study
375	*M. nilagirica*	SDBDU 2015.3027	MZ156335	India: Kerala: Keralamedu	Present study
376	*M. nilagirica*	SDBDU 2014.2612	MZ156336	India: Kerala: Wayanad	Present study
377	*M. nilagirica*	SDBDU 2003.1993	MZ156337	India: Kerala: Suganthagiri	Present study
378	*M. nilagirica*	SDBDU 2006.4866	MZ156338	India: Kerala: Suganthagiri	Present study
379	*M. nilagirica*	SDBDU 2012.2219	MZ156339	India: Karnataka: Gallebedu	Present study
380	*M. nilagirica*	SDBDU 2012.2229	MZ156340	India: Karnataka: Yevakapady	Present study

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No.	Species	Voucher No.	Accession No.	Locality	Reference
381	*M. nilagirica*	SDBDU 2002.1445	MZ156341	India: Karnataka: Madikeri	Present study
382	*M. nilagirica*	SDBDU 2011.65	MZ156342	India: Karnataka: Kottigehara	Present study
383	*M. nilagirica*	SDBDU 2011.97	MZ156343	India: Karnataka: Bhagamandala	Present study
384	*M. nilagirica*	SDBDU 2011.518	MZ156344	India: Karnataka: Bygoor	Present study
385	*M. nilagirica*	SDBDU 2012.2181	MZ156345	India: Karnataka: Mudigere	Present study
386	*M. nilagirica*	SDBDU 2012.2201	MZ156346	India: Karnataka: Shiradi ghats	Present study
387	*M. nilagirica*	SDBDU 2012.2202	MZ156347	India: Karnataka: Sakleshpur	Present study
388	*M. nilagirica*	030607-01	AB167946	India: Karnataka: Madikeri	Kurabayashi *et al.*, 2005
389	*M. nilagirica*	BNHS 4646 / 20-7-June-2003	AB488896	India: Karnataka: Madikeri	Kotaki *et al.*, 2010
390	*M. nilagirica*	BNHS 4645	AB355833	India: Karnataka: Madikeri	Kuramoto *et al.*, 2008 "2007"
391	*M. nilagirica*	BNHS 4647	AB355834	India: Karnataka: Madikeri	Kuramoto *et al.*, 2008 "2007"
392	*M. nilagirica*	SDBDU 2014.2716	MZ156348	India: Kerala: Mattupetty	Present study
393	*M. nilagirica*	SDBDU 2014.2717	MZ156349	India: Kerala: Mattupetty	Present study
394	*M. nilagirica*	SDBDU 2017.3658	MZ156350	India: Kerala: Eravikulam NP	Present study
395	*M. nilagirica*	SDBDU 2016.3414	MZ156351	India: Karnataka: Kudremukh NP	Present study
396	*M. nilagirica*	BNHS 4648	AB355835	India: Karnataka: Mudigere	Kuramoto *et al.*, 2008 "2007"
397	*M. nilagirica*	SDBDU 2016.3208	MZ156352	India: Kerala: Kurchermala	Present study
Outgroup					
398	*Limnonectes khasianus*	haplotype: 16S-lati	AB277306	Malaysia	Kotaki *et al.*, 2008